

***Diaceratherium lemanense* (Rhinocerotidae) from Eschenbach (eastern Switzerland): systematics, palaeoecology, palaeobiogeography**

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With 9 figures and 10 tables

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Abstract: This paper describes a juvenile rhinocerotid skull from Eschenbach (eastern Switzerland). Computed tomography revealed the presence of the unerupted adult teeth P4 and M3 and enabled their three dimensional virtual reconstruction. The morphological features of this skull (postglenoid and posttympanic apophyses in contact, deep nasal notch, very slight occipital elevation, molar lingual cingulum absent, strong molar crochet) ascribe it to an evolved form of *Diaceratherium lemanense* (POMEL 1853) when compared with other European specimens. The diacerathere lineage is restricted to the Western European basins, except for the occurrences of the primitive *D. cf. lamilloquense* in the late Oligocene deposits of Nong Ya Plong (Thailand, Asia) and *Diaceratherium askazansorense* in the early Miocene of the Askazansor Formation (south-western Betpakdala, southern Kazakhstan, Asia). The Eschenbach locality represents a new biostratigraphical pinpoint at the Aquitanian (early Miocene), probably at the base of the MN2a Mammal Zone (*Granitischer Sandstein* Formation, upper part of the Lower Freshwater Molasse, USM, eastern Swiss Molasse Basin). A review of the European diacerathere record is proposed from the First Appearance Data of *D. lamilloquense* (MP29, La Milloque) to the Last Appearance Data of *D. cf. aurelianense* (MN4b, Eggingen-Mittelhart). During this time interval, the diacerathere lineage points to climatic stress and environmental changes. An ecological and spatio-temporal evolution in three phases between the “Terminal Oligocene Crisis” (disappearance of the rhinocerotid lineage) and the “Proboscidean Datum Event” at the late early Miocene (first European occurrence of the overtaking *Brachypotherium*) is suggested: 1) the *Diaceratherium* genus arrive in Europe during the latest Oligocene (the faunal renewal phase); 2) high diversity of the diacerathere group during the Aquitanian (the diversification phase); 3) wide geographical expansion of the last representatives (*D. aurelianense*) of the lineage during the Burdigalian (the stabilisation & geographical expansion phase).

Key words: Rhinocerotidae, *Diaceratherium*, Oligo–Miocene transition, biostratigraphy, palaeobiogeography, tomography.

1. Introduction

The European diacerathere group was widely spread through the Oligo–Miocene transition. Its systematics is relatively well-known from DEPÉRET & DOUXAMI

(1902), RÉPELIN (1917), DIETRICH (1931), DE BONIS (1973), MICHEL (1983), BRUNET et al. (1987), GINSBURG et al. (1991, 2000) and CERDEÑO (1993), but palaeoecological and palaeobiogeographical approaches are limited. The diaceratheres represent the

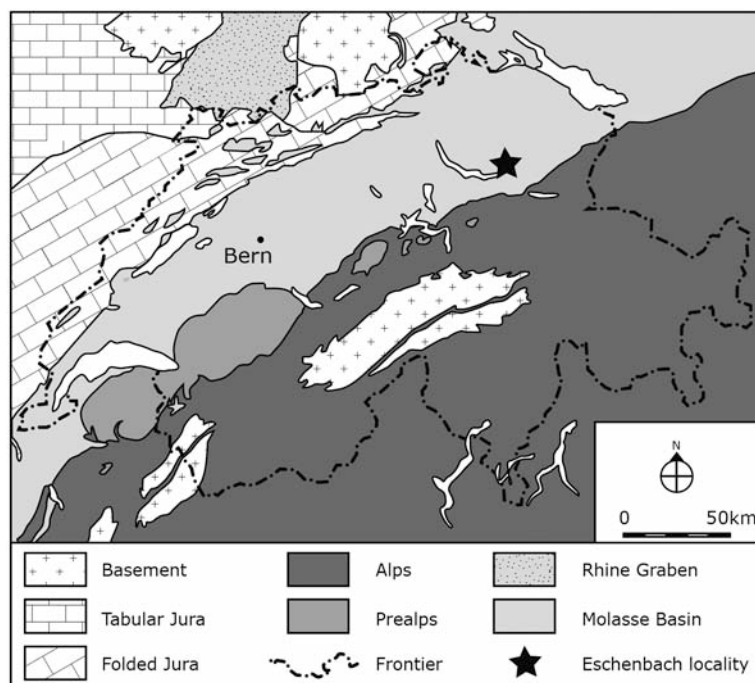
most common group among the large European rhinocerotids during the end of the Oligocene and the beginning of the Miocene (BRUNET et al. 1987, PROTHERO & SCHOCH 1989, PROTHERO et al. 1989, CERDEÑO 1998, HEISSIG 1999, ANTOINE 2002, BECKER 2003). This lineage occurs in Europe after the disappearance of *Ronzotherium romani* from Rickenbach (Switzerland) in MP29, which is the last representative of the ronzothere group (LAD = Last Appearance Data; BRUNET et al. 1987, ENGESSER & MÖDDEN 1997, EMERY 2004, EMERY et al. 2007). The diaceratheres belong to a more advanced group of the Rhinocerotini (ANTOINE 2002), characterised by mediportal and graviportal anatomical types. They seem to be restricted to the Western European basins, except for the occurrence of a *Diaceratherium* cf. *lamilloquense* in the late Oligocene lignite deposits of the Nong Ya Plong Tertiary Basin in Central Thailand (MARIVAUX et al. 2004), which could be the first representative of the group (FAD = First Appearance Data). Furthermore, KORDIKOVA (2001) describes some bone and tooth remains of a new species of diacerather, *Diaceratherium askazansorense*, in the early Miocene of the Askazansor Formation (south-western Betpakdala, southern Kazakhstan, Asia), which currently is the only Miocene representative of the group outside Europe.

Although PROTHERO (1999) suggests that the mammalian fauna shows few short-term responses to climatic events during the Cenozoic, it is nevertheless clear that land plants and other elements of the terrestrial biota are responding. Cause-and-effect relationships between short-term climatic and mammalian faunal changes may exist, but a very high resolved chrono- and biostratigraphy have to be established before these hypotheses can be evaluated. On the other hand, numerous changes in the mammal communities are assumed to be due to sea-level changes, plate tectonics and climatic fluctuations (HOOKER 2000, WHYBROW & ANDREWS 2000). Moreover, some proxies such as body mass, body size, diet, hypsodonty (crown height), locomotion, taxonomical changes, species richness, abundance and commonness to assess the evolutionary responses of mammals to climatic and environmental changes are used by numerous palaeoecological studies (JANIS 1986, LEGENDRE 1989, CERDEÑO & NIETO 1995, JERNVALL & FORTELIUS 2002, JANIS et al. 2004, COSTEUR 2005, FORTELIUS et al. 2006). According to CERDEÑO & NIETO (1995), CERDEÑO (1998) and BECKER (2003) the changes in the composition of

rhinocerotid populations result mainly from climatic and environmental variations, and from competition due to migration.

During the Oligocene, the climate is marked by a slightly progressive degradation, but seems stable with dominating temperate conditions reflected by a relative faunal stability and woodland environments in the northern hemisphere (JANIS 1993). However, some authors (e.g. HAQ et al. 1987, SCHULER 1990, PROTHERO 1994) point out a cooling event in the mid-Oligocene associated with a major sea level regression, but this event was not associated by very significant extinctions. Nonetheless, disappearances (e.g. *Epiaceratherium*, *Gelocus*), regional speciations (e.g., *Eggysodon gaudryi*, *Lophiomeryx chalaniati*, *Ronzotherium romani*), and immigrations (e.g. *Bachitherium*, *Protaceratherium albigense*) can be recognized during the interval MP23–25 in Europe. In addition, the last occurrence of three ruminant families (Bachiteriidae, Gelocidae, Lophiomericidae), the diversification of some rodent groups (e.g. Eomyidae), and the first occurrences of typical late Oligocene mammals as *Microbunodon* or Moschidae (see BRUNET 1979, BLONDEL 1997, UHLIG 1999, ENGESSER & MÖDDEN 1997, VIANEY-LIAUD 2003 and LIHOREAU & DUCROCQ 2007) are observed in MP28. These faunal changes seem to be related to the “Late Oligocene Warming” known from the isotope record (ZACHOS et al. 2001) and the regional temperature peak recorded from palaeofloral data of Central Europe (MOSBRUGGER et al. 2005). After this warming event, numerous authors emphasize a drastic climatic change in Western Europe, starting in the latest Oligocene and marked by a general aridification and cooling (BERGER 1989, 1990a, 1990b, SCHLUNEGGER et al. 2001, BECKER 2003, COSTEUR 2005). This climatic event (“Late Chattian Climatic Crisis” of BECKER 2003, 2004) is herein named the “Terminal Oligocene Crisis” (at ca. 24 Ma) and is essentially linked to disappearances and migrations of large mammals, particularly within the rhinocerotid (disappearance of *Ronzotherium* and arrival of *Diaceratherium*) and anthracotherid lineages (disappearance of *Anthracotherium* and *Microbunodon*). At the global scale a major glaciation at the Oligo/Miocene boundary – which corresponds to a rare orbital congruence involving obliquity and eccentricity – supports the expansion of ice-sheet on Antarctic. This event, called “Mi-1”, marks a fundamental shift in the climate, which accelerates the rates of turnover and speciation in certain groups of biota (ZACHOS et al.

Fig. 1. Geographical and geological setting of the sandstone quarry of Eschenbach (Aquitanian, eastern Switzerland).



2001). During the earliest Miocene the general conditions remain dry but the environments become scattered in mosaic subenvironments (COSTEUR 2005). The environment of Saulcet (MN1, France) is arid and rather closed, whereas the environment of Wischberg (MN1, Switzerland) is clearly open and dry. During the MN2 biozone, the Aquitanian Basin is subdesertic with a vegetation of bushland type, the Massif Central open and humid with a probable vegetation of edaphic grassland type, Switzerland and Germany are covered by more or less arid and closed woodlands, and the Iberian Peninsula landscapes are mostly open and dry. At the late early Miocene, the environments are closed again and associated with a rather wet climate (COSTEUR 2005). However, BÖHME (2003) links the beginning of the “Miocene Climatic Optimum” in Central Europe with two successive migrations (20 Ma and 18 Ma) of ectothermical and thermophile vertebrates adapted to dry conditions. According to TASSY (1989), GÖHLICH (1999) and RÖGL (1999), the initiation of this climatic event occurs just before the palaeobiogeographic “Proboscidean Datum Event” (at ca. 17.5 Ma).

The focus of this study is the description of a new skull of a juvenile *Diaceratherium lemanense* (POMEL 1853) recently discovered in Eschenbach (Canton St. Gallen, Switzerland). By using a computed tomography of unerupted adult teeth, the ontogeny of this

specimen is discussed. The morphometrical and biometrical features of this skull are described as well as its evolutionary state, allowing its identification to an evolved form of *D. lemanense*. Finally the palaeobiogeographical and the palaeoecological evolution of the diaceratheres is clarified (based upon an abundant European fossil record), in order to shed some light on the environmental evolution of the Western European basins during the Oligo–Miocene transition (from the “Terminal Oligocene Crisis” to the “Proboscidean Datum Event”).

2. Geological setting

The Eschenbach locality is a sandstone quarry, near the north-eastern end of the Lake Zürich (eastern Switzerland; Swiss federal coordinates 712.700/232.220), at the southern border of the folded Plateau Molasse, just north of the Subalpine Molasse boundary (Fig. 1). The sandstones are exploited for construction and renovation of buildings by the Müller AG Company (Neuhaus, Canton St. Gallen, Switzerland). Actually, the excavation presents a roughly 60 m deep extraction, exposing subvertical layers of *Granitischer Sandstein* (KAUFMANN 1860). According to HABICHT (1987), the *Granitischer Sandstein* Formation is commonly used for the geological mapping, whereas the *Granitische Molasse* of STUDER (1853)

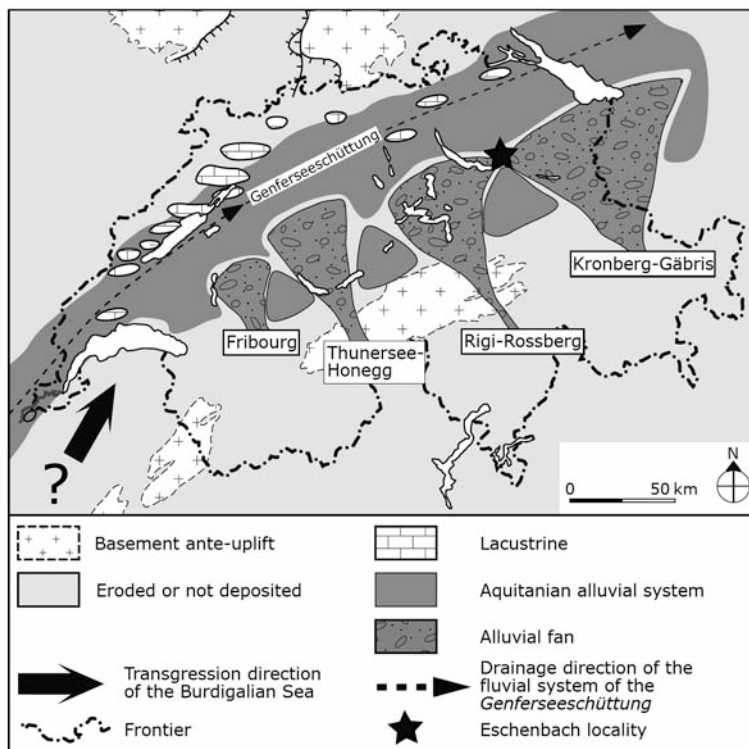


Fig. 2. Palaeogeographical situation of the Swiss Molasse Basin during the Aquitanian (modified after BERGER et al. 2005).

and the *Bollinger Sandstein* of KAUFMANN (1860) are just synonyms. The sandstone deposits of Eschenbach quarry are all dated to the Aquitanian and they belong to the upper part of the USM (*Untere Süßwasser Molasse* = Lower Freshwater Molasse, Chattian–Aquitanian). Palaeogeographically, the Eschenbach locality is located at a triple point, north of the alluvial fans *Rigi-Rossberg Schüttung* and *Kronberg-Gäbris Schüttung*, and south of the vast Aquitanian fluvial system of the *Genferseeschüttung* drained eastwards (Fig. 2).

Chattian–Aquitanian mammal localities with precise biostratigraphical data are rare in eastern Switzerland. ENGESSER & MÖDDEN (1997) report Ebnat-Kappel (MP28; FREI 1979, ENGESSER 1990, MÖDDEN 1994) from the *Ebnater Sandstein* Formation (HEIM 1902), while Wintersberg/Trempel (MP30; FREI 1979) and Sparenweid (= Greit, Höhrnen; MN1; SCHLANKE 1974) are both from the *Wintersberg-Schichten* Formation (HABICHT 1945). BECKER (2003) illustrates dental remains of a *Ronzotherium romani* in Rütli bei Schänis (MP29; FREI 1979) also originating from the *Wintersberg-Schichten* Formation. Moreover, an unpublished mandible of a chalicothere discovered near Bollingen (3 km west of Eschenbach), from the same lithostratigraphical level than the reported skull,

is stored in the collection of the *Paläontologisches Institut und Museum* of the University of Zürich (Heinz Furrer, pers. comm.). The Eschenbach locality is also of biostratigraphical interest for the Aquitanian of the eastern part of the Swiss Molasse Basin and has implications for diaceratherine palaeobiogeography.

3. Material and methods

3.1. Material

The reported material is a complete juvenile skull of a *Diaceratherium lemanense* (NMSG-P2006/1), stored in the collection of the Naturmuseum of St. Gallen (Switzerland). It was discovered by Reto Zwicky (Uznach, St. Gallen, Switzerland), who did a first preparation of the material using relatively coarse tools, as the specimen was initially trapped in a very hard sandstone block. The final preparation was accomplished by one of us (U. O.), using appropriate instruments (e.g. air tool).

3.2. Systematics

The identification is based on anatomical feature descriptions, compared anatomy and biometrical measurements, following the method of GUÉRIN

Table 1. Specimens used for anatomical comparisons.

<i>Diaceratherium</i> species	Locality	Anatomy	Inventory number	Reference	Direct observation	Housing institution
<i>D. lamilloquense</i>	La Milloque (France)	isolated upper teeth	–	DE BONIS 1973, MICHEL 1983	no	Muséum d'histoire naturelle de Marseille, France (UPM)
<i>D. aff. lemanense</i>	Paulhiac (France)	isolated upper teeth	–	DE BONIS 1973, MICHEL 1983	no	Muséum d'histoire naturelle de Marseille, France (UPM)
<i>D. cf. lemanense</i>	Engelalde (Switzerland)	skull	NMBE-D 3193	OOSTER & FISCHER-OOSTER 1871	yes	Naturhistorisches Museum of Bern, Switzerland (NMBE)
<i>D. lemanense</i>	Gannat (France)	skull	–	ROMAN 1911	no	Muséum national d'histoire naturelle de Paris, France (MNHN)
	Saint-Gérard-le-Puy (France)	isolated upper teeth	–	BRUNET et al. 1987	no	unknown
	Cindré (France)	upper jaw	–	ROMAN 1911	no	Baillaud collection in Perfitte-sur-Loire (after ROMAN 1911)
	Eschenbach (Switzerland)	skull	NMSG-P 2006/I	This study	yes	Naturmuseum of St. Gallen, Switzerland (NMSG)
<i>D. asphaltense</i>	Pyrimont-Challonges (France)	skull	UCBL–212997	DEPÉRET & DOUXAMI 1902	yes	Université Claude-Bernard Lyon-Villeurbanne, France (UCBL)
	Saulcet (France)	skull	NMB–SAU 1662	This study	yes	Naturhistorisches Museum of Basle, Switzerland (NMB)
	Wischberg (Switzerland)	skull	NMB–AS75	SCHAUB & HÜRZERLER 1948	yes	Naturhistorisches Museum of Basle, Switzerland (NMB)
<i>D. tomerdingense</i>	Tomerdingen (Germany)	isolated upper teeth	–	DIETRICH 1931	no	Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS)
<i>D. aginense</i>	Laugnac (France)	skull	–	RÉPELIN 1917, DE BONIS 1973, MICHEL 1983	no	Muséum d'histoire naturelle de Marseille, France (UPM)
	Béthusy (Switzerland)	upper jaw	MGL–3356	ENGESSER et al. 1993	yes	Musée cantonal de géologie of Lausanne, Switzerland (MGL)
<i>D. aurelianense</i>	Neuville-aux-Bois (France)	skull	–	NOUEL 1866, CERDEÑO 1993	no	Muséum national d'histoire naturelle de Paris, France (MNHN)

(1980) and the cladistic characters of CERDEÑO (1995) and ANTOINE (2002). The specimens used for comparison and the abbreviations of the housing institutions are listed in Table 1. The other abbreviations are reported in Table 2. All measurements are given with a precision of 0.5 mm.

3.3. Tomography analyses, modelling and rapid prototyping

The computed tomography (CT) was performed on the roughly prepared Eschenbach rhinocerotid skull by the Abteilung Elektronik, Messtechnik, Zuverlässigkeit of the EMPA in Dübendorf (Switzerland). 920 scans were made at 450 kV and at an interval of 0.5 mm. This allowed producing 3D reconstructions of the skull, which was trapped in a 20 cm wide sandstone block. The CT-scans have been processed by

Medical Software Mimics in the Institute for Rapid Product Development (RPD) of St. Gallen (Switzerland). Two types of rapid prototype modelling were performed: a Photopolymer model and a Polyamid-12 model. The details of these analytical methods, not relevant for the present paper, are explained in SCHINDEL et al. (2008). In this study, we describe in the ontogenical analysis two casts of unerupted adult teeth (P4 sin. and M3 sin.), which were made based on the CT 3D reconstructions.

3.4. Locality distribution data

The analysis of the palaeoecological and spatio-temporal evolution of the European diaceratheres is based on 57 *Diaceratherium* localities, recorded in the Iberian Peninsula (Spain and Portugal), France, Switzerland and Germany (Tab. 3). The biostrati-

Table 2. Abbreviations used in this study.

Dentition			
M	upper molar	i	lower inciseive
m	lower molar	D	upper milk tooth
P	upper premolar	d	lower milk tooth
p	lower premolar	TR	tooththrow
I	upper inciseive		
Postcranial skeleton			
Mc	metacarpus	Mt	metatarsus
Biometry			
dext.	right	TD	transversal diameter
sin.	left	abs	absolute
Dist.	distance	anat	anatomic
L	length	TDT	transversal diameter of the astragalus trochlea
W	width		
H	height	TD dia	transversal diameter in the middle of the diaphysis
Index			
I-Gr (Mc)	gracility index based on Mt	I-Hy	hypsodonty index
I-Gr (Mt)	gracility index based on Mc		
Diet			
Br-B	browser brachyodont	Br-H	browser hypsodont
Br-M	browser mesodont	Gr-H	grazer hypsodont

graphy of the localities is updated using recent works of TOBIEN (1980), CERDEÑO (1993), ENGESSER et al. (1993), CERDEÑO & NIETO (1995), HUGUENEY (1997), HEISSIG (1999), ANTOINE et al. (2000), GINSBURG et al. (2000), SACH & HEIZMANN (2001), BECKER (2003), COSTEUR (2005) and FORTELIUS (2003). The sampling includes mainly the common *Diaceratherium* species (*D. lemanense*, *D. asphaltense*, *D. aginense* and *D. aurelianense*). Additionally, the unusual local species *D. lamilloquense* and *D. tomerdingense* are also considered in order to complete the data.

To estimate the sampling effects, the commonness (locality coverage) of the *Diaceratherium* locality record is related to that of 178 large mammal localities and is assessed per million years within the considered biozones. The small mammal localities (no more taxa than rodents, lagomorphs, insectivores and cainotheres) are excluded to even out the sampling bias. The considered stratigraphical interval corresponds to the Oligocene–Miocene transition, from MP29 to MN4. The chronostratigraphy of the MP and MN biozones is calibrated after ENGESSER & MÖDDEN (1997), KEMPF et al. (1997), MEIN (1999), SCHMIDT-KITTLER et al. (1997) and STEININGER (1999). All data on

localities (Tab. 4), species and chronostratigraphical correlations are obtained from the existing database “Neogene of the Old World” (cf. FORTELIUS 2003: NOW public release, July 2003), from the literature (see references in Tabs. 3–4) and also from several unpublished collections from NMB and NMBE (only for the *Diaceratherium* localities).

3.5. Maps

All recorded *Diaceratherium* localities have been plotted on modern maps of Western Europe to illustrate the biogeographical distribution (contractions, expansions, fragmentations). Modern geographical names (Iberian Peninsula, France, Switzerland and Germany) are also used as landmarks, but backgrounds of European Tertiary basins are added for each map to control the sampling effects. Because of the map scale, the localities with very close coordinates are plotted in the same point (see Fig. 6).

3.6. Palaeoecology

A part of the specimens used for the palaeoecological analyses has been directly studied in the related collections. The data of the other specimens are from the literature. The palaeoecological parameters of *Diaceratherium* species have been characterised in order to define the anatomical types and diets. Following CERDEÑO & NIETO (1995), the body size has been estimated from the transversal diameter of the astragalus trochlea (TDT), which indicates the relative size of the animal (shoulder height). Body mass has been estimated from the m1 area, following the formula of LEGENDRE (1989): $\ln X = \ln Y \times 1.564 + 3.267$, where X = weight and Y = m1 area. Slenderness has been measured mainly from the McIII and secondary from MtIII and McII following the method of the gracility index (GUÉRIN 1980): $100 \times \text{TDDia} / L$. The diets have been estimated thanks to the description of the patterns of the back tooth occlusal view and by calculating the upper back tooth hypsodonty index (*sensu* GUÉRIN 1980, on P3-M2 for more reliable results: $100 \times H / L$). According to FORTELIUS et al. (2006), brachyodont teeth have a ratio less than 80, mesodont are in the range of 80–120 and hypsodont over 120. The head holding (feeding posture) is a function of the feeding behaviour, which can be characterised from skulls, by using the occipital side inclination and the angle of the occipital crest in lateral view (BALES 1996). The different categories of palaeoecological parameters are exposed in Table 5.

Table 3. Biostratigraphical distribution of the European *Diaceratherium* localities.

<i>Diaceratherium</i> species	Biostratigraphy	Locality	Region	Country	References
<i>D. cf. aurelianense</i> (Nouel, 1866)	MN4b	57 Eggingen-Mittelhart 3	Bayern	Germany	SACH & HEIZMANN 2001
<i>D. aurelianense</i> (Nouel, 1866)	MN4a	56 Artenay	Loiret	France	GINSBURG 1989a, 1989b, CERDEÑO 1993, ANTOINE et al. 2000, FORTELIUS 2003
	MN4a	55 Montréal-du-Gers	Lot-et-Garonne	France	ANTOINE et al. 2000, FORTELIUS 2003
	MN4a	54 Rubielos de Mora	Terruel	Spain	CERDEÑO 1992, CERDEÑO & NIETO 1995, MONTOYA et al. 1996, FORTELIUS 2003
	MN3	53 Cheyre Pra Bosset	Fribourg	Switzerland	BECKER 2003, BERGER (pers. comm.), coll. NMB
	MN3	52 La Molière	Fribourg	Switzerland	BECKER 2003, FORTELIUS 2003
	MN3	51 Brüttelen 1	Bern	Switzerland	BECKER 2003, BERGER (pers. comm.), coll. NMB
	MN3	50 Neuville-aux-Bois	Loiret	France	NOUEL 1866, MAYET 1908, CERDEÑO 1993, HEISSIG 1999, ANTOINE et al. 2000, FORTELIUS 2003
	MN3	49 Chilleurs-aux-Bois	Loiret	France	MAYET 1908, CERDEÑO 1993, ANTOINE et al. 2000, FORTELIUS 2003
	MN3	48 Mauvières	Indre-et-Loire	France	GINSBURG et al. 2000
	MN3	47 Esvres	Indre-et-Loire	France	GINSBURG 1988, FORTELIUS 2003
	MN3	46 Les Beilleaux	Indre-et-Loire	France	GINSBURG et al. 1981, ANTOINE et al. 2000, FORTELIUS 2003
	MN3	45 Pontigné	Maine-et-Loire	France	GINSBURG & BONNEAU 1995
	MN3	44 La Brosse	Maine-et-Loire	France	GINSBURG et al. 2000
	MN3	43 Chitenay	Loir-et-Cher	France	GINSBURG et al. 2000
	MN3	42 Ronville	Loiret	France	coll. NMB, MENNECART (pers. comm.)
	MN3	41 Beaulieu	Bouches-du-Rhône	France	AGUILAR et al. 2003, GINSBURG 2005
	MN3	40 Navère	Gers	France	ANTOINE et al. 2000, FORTELIUS 2003
	MN3	39 Marsolan	Gers	France	ANTOINE et al. 2000, FORTELIUS 2003
	MN3	38 Wintershof-West	Bayern	Germany	AGUILAR et al. 2003
	MN3	37 Molí Calopa	Valles-Penedes	Spain	CERDEÑO 1992, CERDEÑO & NIETO 1995
	MN3	36 Horta das Tripas	Vale do Tejo	Portugal	GINSBURG & ANTUNES 1979
<i>D. cf. aurelianense</i> (Nouel, 1866)	MN2b	35 Loranca	Loranca	Spain	CERDEÑO 1992, CERDEÑO & NIETO 1995
<i>D. askazansorense</i>	MN2-3	– Askazansor	Betpakdala	Kazakhstan	KORDIKOVA 2001
<i>D. aginense</i> (Répelin, 1917)	MN2b	34 Hessler	Nordrhein-Westfalen	Germany	TOBIEN 1980, HEISSIG 1999
	MN2b	33 Laugnac	Lot-et-Garonne	France	DE BONIS 1973, HEISSIG 1999, FORTELIUS 2003
	MN2a	32 Rovéréaz	Vaud	Switzerland	ENGESSER et al. 1993
	MN2a	31 Chemin des Falaises	Vaud	Switzerland	ENGESSER et al. 1993, FORTELIUS 2003
	MN2a	30 Haut du Calvaire	Vaud	Switzerland	ENGESSER et al. 1993, FORTELIUS 2003
	MN2a	29 La Chaux 7	Vaud	Switzerland	BECKER 2003
	MN2a	28 Béthusy	Vaud	Switzerland	ENGESSER et al. 1993
	MN2a	27 Le Tunnel	Vaud	Switzerland	ENGESSER et al. 1993, FORTELIUS 2003
	MN2a	26 Morrens	Vaud	Switzerland	ENGESSER et al. 1993
	MN2a	25 Maupas	Vaud	Switzerland	ENGESSER et al. 1993
	MN2a	24 Moulin d'Assens	Vaud	Switzerland	ENGESSER et al. 1993
<i>D. tomerdingense</i> (Dietrich, 1931)	MN1	23 Tomerdingen 2	Baden-Württemberg	Germany	DIETRICH 1931, HEISSIG 1999
<i>D. asphaltense</i> (Depéret, 1902)	MN1	– Wischberg	Bern	Switzerland	SCHAUB & HÜRZELER 1948, coll. NMB, coll. NMBE
	MN1	– Saulcet	Allier	France	HUGUENY 1997, coll. NMB
	MN1	22 Pyrimont-Challonges	Ain	France	DEPÉRET & DOUXAMI 1902, HEISSIG 1999

The dietary subdivisions used in this paper are mainly based on those of JANIS (1986). We consider grazing rhinocerotids (at least 90% of the year round diet in form of monocotyledonous grass materiel) and

browser rhinocerotids (at least 90% of the year round diet in form of dicotyledonous herbage). The latter are tree and shrub foliage eaters and are divided into “high browsers feeding above ground level” and

Table 3. (continued)

<i>D. lemanense</i> (Pomel, 1853)	MN2b	21	Budenheim	Mainz	Germany	ROMAN, 1924, TOBIEN 1980
	MN2b	20	Barbotan-les-Thermes	Gers	France	GINSBURG et al. 1991
	MN2b	19	Selles-sur-Cher	Loir-et-Cher	France	ROMAN 1911, GINSBURG & HUGUENEY 1980
evolved form	MN2a	18	Eschenbach	St. Gallen	Switzerland	this study
evolved form	MN2a	17	Montaigu-le-Blin	Allier	France	HUGUENEY 1997, FORTELIUS 2003, coll. NMB
evolved form	MN2a	16	Saint-Gérard-le-Puy	Allier	France	BRUNET et al. 1987, HUGUENEY 1997
	MN2	15	Michelsberg	Bayern	Germany	DIETRICH 1931, FORTELIUS 2003
primitive form	MN1-2	14	Cindré	Allier	France	ROMAN 1911, HUGUENEY 1997
	MN1	13	Oppenheim	Mainz	Germany	TOBIEN 1980
	MN1	12	Weisenau	Mainz	Germany	TOBIEN 1980, FORTELIUS 2003
	MN1	11	Finthen	Mainz	Germany	TOBIEN 1980
	MN1	10	Wischberg	Bern	Switzerland	SCHAUB & HÜRZELER 1948, coll. NMB, coll. NMBE
	MN1	9	Randan	Puy-de-Dôme	France	ROMAN 1911, DE BONIS 1973
primitive form	MN1	8	Saulcet	Allier	France	HUGUENEY 1997, coll. NMB
	MN1	7	Gannat	Allier	France	DUVERNOY 1853, ROMAN 1911, LAVOCAT 1951, FORTELIUS 2003, coll. NMB
	MN1	6	Métro de Toulouse	Haute-Garonne	France	ANTOINE ET AL. 2006
<i>D. cf. lemanense</i> (Pomel, 1853)	MN1-2	5	Engelhalde	Bern	Switzerland	OOSTER & FISCHER-OOSTER 1871, STEHLIN 1914, BECKER 2003, coll. NMBE
<i>D. lemanense</i> (Pomel, 1853)	MP30	4	Rott bei Bonn	Nordrhein-Westfalen	Germany	VON KOENIGSWALD ET AL. 1992, MÖRS 2002
<i>D. aff. lemanense</i> (Pomel, 1853)	MN1	3	Paulhiac	Lot-et-Garonne	France	DE BONIS 1973, BRUNET et al. 1987, FORTELIUS 2003
	MP30	2	Thézels	Lot	France	MICHEL 1983, BRUNET et al. 1987
<i>D. lamilloquense</i> (Michel, 1983)	MP29	1	La Milloque	Lot-et-Garonne	France	MICHEL 1983, BRUNET et al. 1987
<i>D. cf. lamilloquense</i> (Michel, 1983)	Late Oligocene	-	Nong Ya Plong	Phetchaburi Province	Thailand	MARIVAUX et al. 2004

“regular browsers feeding both above the ground and at ground level”. Finally the intermediate feeders are defined as “mixed feeders” living in open habitats (savanna or prairie) or in closed habitats (bushland, woodland or forest).

To test the above methods, they were also applied to the extant rhinoceroses (4 genera, 5 species) and compared with the literature data from NOWAK (1999) and CHRISTIANSEN (2002). Except for the method of LEGENDRE (1989) – in which the estimated weights are generally higher, in particular for the relatively slender and large *Diceros bicornis* –, all methods match well with the five extant species. Among the fossil rhinocerotids, the weight estimates are probably considerably too high for the *Ronzotherium* species (slender and cursorial anatomical types). The Legendre’s method seems not to be adequate for the slender forms ($r^2 = 0.521$), but it provides useful data for the mediportal and graviportal anatomical types ($r^2 = 0.8473$). The regression of body mass on skull length (occipital condyles-premaxilla) shows a better

correlation ($r^2 = 0.9242$), but the material does not always allow this measurement, therefore it has only been considered for the extant *D. bicornis* and for the extinct *Ronzotherium* species. Finally, the different anatomical types and diets defined for each *Diaceratherium* species and extant rhinoceroses have been compared in order to highlight analogies of the ecological parameters.

4. Results

4.1. Systematics

The suprageneric arrangement follows that proposed by ANTOINE (2002).

Order Perissodactyla OWEN 1848
 Family Rhinocerotidae GRAY 1821
 Subfamily Rhinocerotinae GRAY 1821
 Tribe Rhinocerotini GRAY 1821
 Subtribe Teleoceratina HAY 1902
 Genus *Diaceratherium* DIETRICH 1931

Table 4. Biostratigraphical distribution of the European large mammal localities.

Iberian Peninsula	MN4	nM=32	Acacias (CERDEÑO & NIETO 1995)	El Casots (GENTRY et al. 1999)	Munébrega 1-3, AB (CERDEÑO & NIETO 1995)
			Armantes I (DAAMS et al. 1977)	Lisboa (CERDEÑO 1992)	PAR-Pennelas (FORTELIUS 2003)
			Artesilla (CERDEÑO & NIETO 1995)	Puente Toledo (CERDEÑO & NIETO 1995)	Paseo de las Acacias (FORTELIUS 2003)
			Buñol (GÖHLICH 1999)	Quinta da Farinheira (GÖHLICH 1999)	Rubielos de Mora (MONTROYA et al. 1996)
			Can Canals (FORTELIUS 2003)	Quinta da Noiva (VAN DER MADE 1999)	Sant Mammet (COSTEUR 2005)
			Can Julia (CERDEÑO & NIETO 1995)	Quinta das Pedreiras (GÖHLICH 1999)	Tarazona (GENTRY et al. 1999)
			Can Mas (CERDEÑO & NIETO 1995)	Quinta do Narigao (VAN DER MADE 1999)	Tarrabla V (CERDEÑO & NIETO 1995)
			Charneca de Lumiar (HEISSIG 1999)	Quinta Grande (GÖHLICH 1999)	Torrijos (CERDEÑO & NIETO 1995)
			Conrelas do Cavao (GÖHLICH 1999)	La Retama (CERDEÑO & NIETO 1995)	Valdemoros 1a, 1b (CERDEÑO & NIETO 1995)
			Córcoles (GÖHLICH 1999)	Monteagudo (FORTELIUS 2003)	Villafeliche (FORTELIUS 2003)
			El Canyet (FORTELIUS 2003)	Moratines (FORTELIUS 2003)	
	MN3	nM=9	Agreda (FORTELIUS 2003)	Horta dos Tripas (VAN DER MADE 1999)	Nasa (MURELAGA et al. 2004)
			Colmenar (FORTELIUS 2003)	Molí Calopa (CERDEÑO & NIETO 1995)	San Andres de la Barca (FORTELIUS 2003)
			Costa Blanca (FORTELIUS 2003)	Moratilla (MORALES & SORIA 1984)	Tudela (FORTELIUS 2003)
	MN2	nM=8	Cabeza de la Junta (MURELAGA et al. 2004)	Loranca (CERDEÑO & NIETO 1995)	Remblar (MORALES & SORIA 1984)
			Cetina de Aragon (CERDEÑO & NIETO 1995)	Moheda (FORTELIUS 2003)	Valquemado (CERDEÑO & NIETO 1995)
			Le Encinilla (QUIRALTE & MORALES 2006)	Navarrete del Rio (GENTRY et al. 1999)	
	MN1	nM=0	—	—	—
	MP30	nM=0	—	—	—
	MP29	nM=0	—	—	—
France	MN4	nM=17	Aérottrain (ANTOINE et al. 2000)	Bourg-Saint-Bernard (FORTELIUS 2003)	Pont Boutard (VAN DER MADE 1999)
			Artenay (ANTOINE et al. 2000)	Captieux (FORTELIUS 2003)	Pont du Manne (HEISSIG 1999)
			Autrive (FORTELIUS 2003)	Chevilly (CERDEÑO 1993)	La Romieu (ANTOINE et al. 2000)
			Baigneaux (ANTOINE et al. 2000)	Monbrun (FORTELIUS 2003)	La Sauvetat (FORTELIUS 2003)
			Le Baradieu (COSTEUR 2005)	Montréal-du-Gers (ANTOINE et al. 2000)	Vieux Collonges (FORTELIUS 2003)
			Bézian (ANTOINE et al. 2000)	Pellicahus (ANTOINE et al. 2000)	
	MN3	nM=15	Beaulieu (GINSBURG 2005)	Contres (FORTELIUS 2003)	Le Mazet (GÖHLICH 1999)
			Les Beilleaux (ANTOINE et al. 2000)	Estrepouy (ANTOINE et al. 2000)	Navère (ANTOINE et al. 2000)
			La Brosse (GINSBURG et al. 2000)	Esvres (GINSBURG 1988)	Neuville-aux-Bois (ANTOINE et al. 2000)
			Chilleurs-aux-Bois (ANTOINE et al. 2000)	Marsolan (ANTOINE et al. 2000)	Pontigné (GINSBURG & BONNEAU 1995)
			Chitenay (GINSBURG et al. 2000)	Mauvière (GINSBURG et al. 2000)	Ronville (coll. NMB)
	MN2	nM=8	Barbotan-les-Thermes (GINSBURG et al. 1991)	Laugnac (DE BONIS 1973)	Saint-Gérard-le-Puy (HUGUENEY 1997)
			Chavroches (HUGUENEY 1997)	Moissac (CERDEÑO 1992)	Selles-sur-Cher (HEISSIG 1999)
	MN1	nM=9	Gans (COSTEUR 2005)	Montaigu-le-Blin (HUGUENEY 1997)	
			Cindré (HUGUENEY 1997)	Pauhliac (DE BONIS 1973)	Randan (DE BONIS 1973)
			Gannat (HUGUENEY 1997)	Pechbonieu (CERDEÑO 1992)	Roche-Blanche-Gergovie (HUGUENEY et al. 1999)
	MP30	nM=4	Méto Toulouse (ANTOINE et al. 2006)	Pyrumont-Challonges (HEISSIG 1999)	Saulcet (HUGUENEY 1997)
			Coderet (HUGUENEY 1997)	Peublan (HUGUENEY 1997)	
			Dieupentale (COSTEUR 2005)	Thézels (BRUNET et al. 1987)	
	MP29	nM=5	Chaufours (HUGUENEY 1997)	La Milloque (BRUNET et al. 1987)	Verneuill (HUGUENEY 1997)
			Cournon (HUGUENEY 1997)	Mine des Roys (HUGUENEY 1997)	

Table 4. (continued)

Switzerland	MN4	nM=3	Benken (BECKER 2003)	Glovelier (KÄLIN 1997)	Tägernastrasse (KÄLIN 1997)
	MN3	nM=6	Bierkeller (KÄLIN 1997)	Goldinger Tobel 1 (KÄLIN 1997)	La Molière (BECKER 2003)
			Brüttelen 1 (KÄLIN 1997)	Cheyres Pra Bosset (BECKER 2003)	Trub-Sältenbach (KÄLIN 1997)
	MN2	nM=16	Béthusy (ENGESSER et al. 1993)	Maupas (ENGESSER et al. 1993)	La Solitude (ENGESSER et al. 1993)
			La Borde (ENGESSER et al. 1993)	Morrens (ENGESSER et al. 1993)	Le Tunnel (ENGESSER et al. 1993)
			La Chau 7 (KÄLIN 1997)	Moulin d'Assens (ENGESSER et al. 1993)	Le Valentin (ENGESSER et al. 1993)
			Ch. des Falaises (ENGESSER et al. 1993)	Petites Roches (ENGESSER et al. 1993)	Wallenried (BECKER et al. 2001)
			Eschenbach (this study)	Richemont (ENGESSER et al. 1993)	
			Haut du Calvaire (ENGESSER et al. 1993)	Rovéréaz (ENGESSER et al. 1993)	
	MN1	nM=4	Engelhalde (BECKER 2003)	Wischberg (SCHAUB & HÜRZELER 1948)	
			Formant 11, 13 (ENGESSER & MÖDDEN 1997)	Zürchermühle (VAN DER MADE 1999)	
	MP30	nM=2	Haslen (SCHAUB 1928)	Küttigen (ENGESSER & MÖDDEN 1997)	
	MP29	nM=4	Brochene Fluh 19/20 (ENGESSER & MÖDDEN 1997)	Rochette (BERGER 1998)	Rüf bei Schänis (BECKER 2003)
			Rickenbach (ENGESSER & MÖDDEN 1997)		
Germany	MN4	nM=12	Baggersee Freudenegg (SACH & HEIZMANN 2001)	Grimmelfingen (SACH & HEIZMANN 2001)	Langenau 1, 2 (SACH & HEIZMANN 2001)
			Eggingen-Mittelhart 3 (SACH & HEIZMANN 2001)	Günzburg (et GENTRY et al. 1999)	Petersbuch (COSTEUR 2005)
			Engelwies (FORTELIUS 2003)	Illerkirchberg 1 (SACH & HEIZMANN 2001)	Rauscheröd (GENTRY et al. 1999)
			Erkertshofen 2 (COSTEUR 2005)		Ravenburg (FORTELIUS 2003)
			Gerlenhofen (SACH & HEIZMANN 2001)		
	MN3	nM=1	Wintershof-West (AGUILAR et al. 2003)		
	MN2	nM=12	Budenheim (TOBIEN 1980)	Hochheim-Flörshcim (TOBIEN 1980)	Ulm- Eselberg (VON KÖNIGSWALD 1930)
			Eggingen (VON KÖNIGSWALD 1930)	Mischelsberg (DIETRICH 1931)	Ulm-Liesberg (FORTELIUS 2003)
			Frankfurt (TOBIEN 1980)	Pappenheim (HEISSIG 1999)	Ulm-Klinik (FORTELIUS 2003)
			Hessler (TOBIEN 1980)	Ulm (HEISSIG 1999)	Ulm-Westtangente (FORTELIUS 2003)
	MN1	nM=8	Altheim-Breitenlauh (SACH & HEIZMANN 2001)	Lautern 2 (COSTEUR 2005)	Treuchlingen 2 (COSTEUR 2005)
			Finthen (TOBIEN 1980)	Oppenheim (TOBIEN 1980)	Weissenau (TOBIEN 1980)
	MP30	nM=2	Flörshcim (TOBIEN 1980)	Tomerdingen 2 (HEISSIG 1999)	Weissenburg 6 (COSTEUR 2005)
	MP29	nM=1	Herlingen (COSTEUR 2005)	Rott bei Bonn (VON KOENIGSWALD et al. 1992)	

Type species: *Diaceratherium tomerdingense* (DIETRICH 1931).

Included species: *Diaceratherium lamilloquense* MICHEL 1983; *Diaceratherium lemanense* (POMEL 1853); *Diaceratherium asphaltense* (DEPÉRET & DOUXAMI 1902); *Diaceratherium tomerdingense* DIETRICH 1931; *Diaceratherium aginense* (RÉPELIN 1917); *Diaceratherium askazansorense* KORDIKOVA 2001; *Diaceratherium aurelianense* (NOUEL 1866). Contrary to LAVOCAT (1951) and HEISSIG (1999), we do not use the genus *Brachydiceratherium* (LAVOCAT 1951) for the species *D. lemanense*.

Diaceratherium lemanense (POMEL 1853)

Synonymy list

- 1834 Very large *Lophiodon* from Gannat – CUVIER: 414-417.
- 1839 *Rhinoceros incisivus* KAUP – DE BLAINVILLE: pl. IX, X, XII.
- 1853 *Acerotherium lemanense* – POMEL: 77.
- 1853 *Acerotherium gannatense* – DUVERNOY: 51-70; pl. V; pl. VI, fig. 1, 2, 3, 10, 12, 18; pl. VII, fig. 2.
- 1853 *Rhinoceros* from Randan – DUVERNOY: 47-50; pl. VII, fig. 3; pl. VIII, fig. 5.

Table 5. Categories of the different palaeoecological parameters used in this study.

Body size	TDT	Shoulder height
small	<50	< 1.0 m
medium-small	50-60	1.0 – 1.5 m
medium-large	60-70	1.5 m – 1.8 m
large	> 70	> 1.8 m
Body mass	Weight	
small	< 1000 kg	
medium-small	1000-1500 kg	
medium-large	1500-2000 kg	
large	> 2000 kg	
Slenderness	I-Gr (McIII)	
cursorial	< 25	
mediportal	25-30	
graviportal	> 30	
Diet	I-Hy	Feeding category
brachyodont	< 80	folivore
mesodont	80-120	folivore
hypsodont	> 120	mixed feeder-grazer
Feeding behaviour	Head holding (= feeding posture)	Herbivore category
possibly specialized in short vegetation	head posture down	regular browser/grazer
indiscriminate	head posture intermediate	regular browser
specialized in tall vegetation	head posture up	high browser

is dolichocephalic (maximum zygomatic width/nasal-occipital length ratio = 0.43). The nasal bones are fine and long. The premaxilla is also fine, very slightly longer than the nasals, and shows a marked upward vertical displacement at the anterior edge of the D1. The zygomatic arch is low in its anterior part, but slightly elevated with a flexure form, and weakly broader in its posterior part. The dorsal profile of the skull is mainly flat and characterised by a nasal tip pointing downwards, a slight dome at the nasal posterior part, a shallow frontal depression, a very slight occipital elevation, an acute occipital angle and an occipital side inclined backwards. The postglenoid and posttympanic apophyses are in contact, and the former is curved forwards. The back of the toothrow reaches the posterior half of the skull. The nasal notch is deep, U-shaped, marked by a small nick at the nasal tip and reaches the posterior edge of the P3 while the anterior border of the orbit is above the anterior edge of the M1. The minimal distance between the posterior edge of the nasal notch and the anterior border of the orbit is 53.0 mm. In dorsal view, the nasal bones are not fused. No rough spots for nasal or frontal horns are identified. The postorbital constriction is strong, marked by very little separated fronto-parietal crests (minimum distance = 18.0 mm). The biometrical dimensions of the Eschenbach skull are shown in Table 6.

- 1900 *Aceratherium lemanense* POMEL – OSBORN: 243; fig. 8b.
 1911 *Acerotherium lemanense* POMEL – ROMAN: 58-64; pl. VII; pl. VIII, fig. 1, 1a, 1b, 2, 2a, 3.
 1924 *Aceratherium lemanense* POMEL – ROMAN: 48-51; fig. 22-25.
 1951 *Diceratherium* (*Brachydiceratherium*) *lemanense* POMEL – LAVOCAT: 113-115.
 1973 *Brachypotherium lemanense* POMEL – DE BONIS: 123-128; fig. 26.3, 27.1, 29.2, 31.1, 32.2, 33.5.
 1982 *Diaceratherium lemanense* POMEL – GINSBURG et al.: 403-406.
 1983 *Diaceratherium lemanense* POMEL – MICHEL: 135-147.
 1987 *Diaceratherium lemanense* POMEL – BRUNET et al.: 64; pl. 1, fig. 1, 7, 8, 12.
 1999 *Brachydiceratherium lemanense* POMEL – HEISSIG: 181-182, 187.

Description: Skull (Fig. 3). The Eschenbach skull (NMSG-P2006/1), complete and very few deformed, belongs to a juvenile. The general outline of the skull

Dentition (Fig. 4c). The anterior set of teeth is composed by the unique I1 and the back toothrow by the series D1-P2-P3-D4-M1-M2. The computed tomography points out the presence of the unerupted P4 and M3, but does not reveal any evidence for an unerupted P1. The paracone folding and the parastylic groove are well marked from the P3 to the M2. The lingual cingulum is strong and continuous on premolars. There are no enamel foldings on the crowns and no traces of cement. The crowns of the back teeth are rather high (mesodont state). The biometrical dimensions of the teeth and the hypsodonty index are given in Table 7.

Upper anterior teeth. The I1 are small with a low crown and a flattened elliptic shape of the crown cross section. The lingual face is larger than the labial one.

Upper milk teeth. The D1 has a subtriangular shape, a rounded ectoloph without marked foldings, a labial cingulum (well marked under the metacone) and a posterior cingulum delimiting a little postfossette. The D4 exhibits a quadrangular shape, a marked paracone folding, and well-developed parastyle and metastyle.

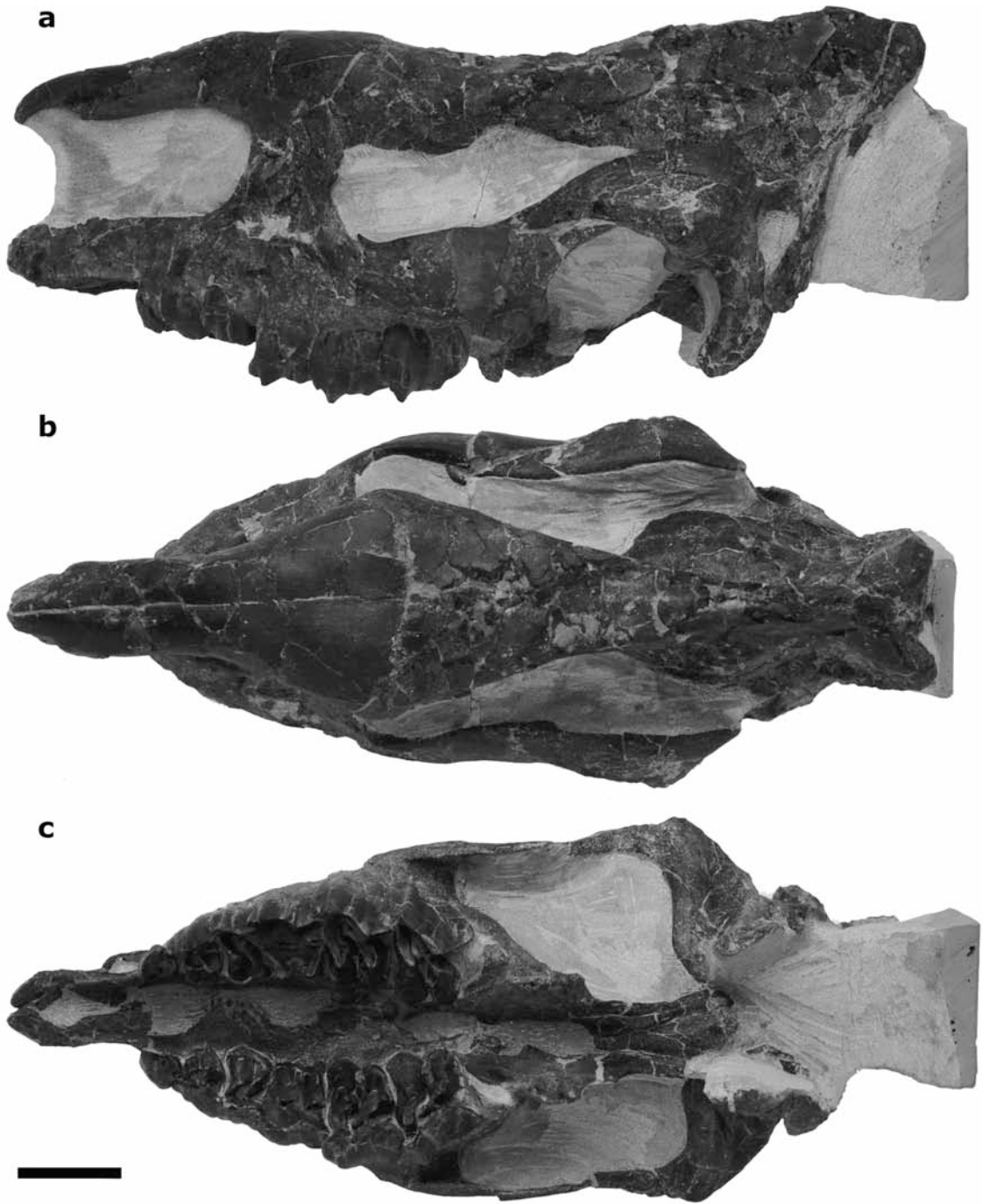


Fig. 3. Skull (NMSG-P2006/1) of *Diaceratherium lemanense* (POMEL, 1853) from the Aquitanian of Eschenbach (St. Gallen, Switzerland); **a:** left lateral view; **b:** dorsal view; **c:** palatine view. Scale bar: 5 cm.

Upper premolars. The upper premolars are characterised by a rather flat ectoloph with a relatively weak paracone folding on the P2 but more marked on the P3. The outlines vary from trapezoidal for the P2

to rectangular for the P3. A crista and a crochet are developed and fused in depth, delimiting a pseudo-medifossette. The metaloph is oblique, forming an angle at the starting of crochets. The protoloph and the

Table 6. Biometrical dimensions of the *Diaceratherium* skulls. The data in italics are from the literature.

Skull dimensions	<i>Diaceratherium lemanense</i> Gannat ROMAN 1911	<i>D. lemanense</i> Eschen- bach NMSG– P2006/1	<i>D. cf. lemanense</i> Engelhalde NMBE– D3193 OOSTER & FISCHER– OOSTER 1871	<i>D. asphaltense</i> Pyrimont– Challonges UCBL– 212997 DEPÉRET & DOUXAMI 1902	<i>D. asphaltense</i> Wischberg NMB–AS75	<i>D. asphaltense</i> Saulcet NMB–SAU 1662	<i>D. aginense</i> Laugnac RÉPELIN 1917	<i>D. aurelianense</i> Neuville-aux- Bois NOUEL 1866 CERDEÑO 1993
Dist. occipital condyles-premaxill	554.0	–	–	–	640.0	630.0	–	–
Dist. occipital condyles-nasal	539.0	–	–	625.0	595.0	610.0	–	–
Dist. occipital crest-nasal	509.0	435.0	490.0	(590.0)	–	555.0	545.0	495.0
L nasal notch	167.5	122.0	175.0	193.0	170.0	178.0	180.0	160.0
W min. posterior skull	–	(40.0)	45.0	(70.0)	–	42.0	–	169.0
Dist. occipital crest-post-orbital processus	–	220.0	–	305.0	–	–	–	266.0
Dist. occipital crest-sus-orbital processus	–	260.0	–	325.0	–	320.0	340.0	–
Dist. occipital crest-ante-orbital processus	324.0	280.0	–	360.0	–	360.0	–	–
Dist. nasal opening-anterior border of orbit	52.5	53.0	75.0	85.0	80.0	78.0	–	85.0
Dist. posterior face M3-condyle	193.0	–	–	260.0	280.0	280.0	–	–
Dist. nasal-orbit	220.5	170.0	–	278.0	250.0	245.0	–	–
W occipital crest	(71.5)	66.0	–	(130.0)	(180.0)	150.0	–	150.0
W mastoid apophyses	(102.0)	119.0	–	175.0	–	215.0	–	265.0
Dist. min. fronto-parietal crests	(10.0)	18.0	34.0	17.0	–	29.0	–	100
W post-orbital processus	150.0	90.0	(134.0)	140.0	110.0	–	–	–
W sus-orbital processus	166.0	111.5	(138.0)	135.0	140.0	165.0	170.0	–
W ante-orbital processus	167.0	123.5	(144.0)	140.0	160.0	175.0	–	–
W max. zygomatic arches	217.0	186.5	(232.0)	(290.0)	–	380.0	340.0	350.0
W above nasal opening	59.0	62.0	–	80.0	(75.0)	100.0	105.0	96.0
H occipital face (sup. border of foramen)	–	–	–	(75.0)	–	130.0	–	–
H occipital face (inf. border of foramen)	–	–	–	–	–	185.0	–	–
H skull above P2	191.0	(122.0)	180.0	100.0	–	160.0	–	–
H skull above P4-M1	195.0	(140.0)	225.0	95.0	(155.0)	185.0	–	–
H skull above middle of M3	157.0	(131.0)	225.0	–	(140.0)	170.0	–	–
W palate between the P2	–	41.5	–	52.5	–	66.0	–	–
W palate between the P4/M1	–	(42.5)	–	69.0	–	80.0	–	–
W palate between the M3	–	–	–	72.0	–	87.5	–	–
TD occipital foramen	–	–	–	48.0	(35.0)	45.0	60.0	53.5
TD occipital condyles	–	–	–	114.5	(112.0)	150.0	–	127.5
Position of the nasal opening	above P3	above P3/P4	above P3	above P3	above P4	above P3	above P4	above P3
Position of the orbit anterior border	above M1	above M1	above P4/M1	above M1	above M2	above M1	above M1/M2	above M1

metaloph are parallel. A posterior cingulum is always present. The lingual cingulum is strong and continuous until the anterior face of the metaloph whilst the labial cingulum is absent. The P2 is semi-molariform with linked protocone and hypocone. The parastyle and metastyle are tapered and elongated in the axis of the ectoloph. The P3 is semi-molariform to

molariform with a weak low lingual bridge between the protocone and the hypocone. The protoloph is slightly longer than the metaloph. The median valley (= medisinus) is S-shaped. Both postfossette and median valley are deep with the same depth. The parastyle is more developed than on the P2.

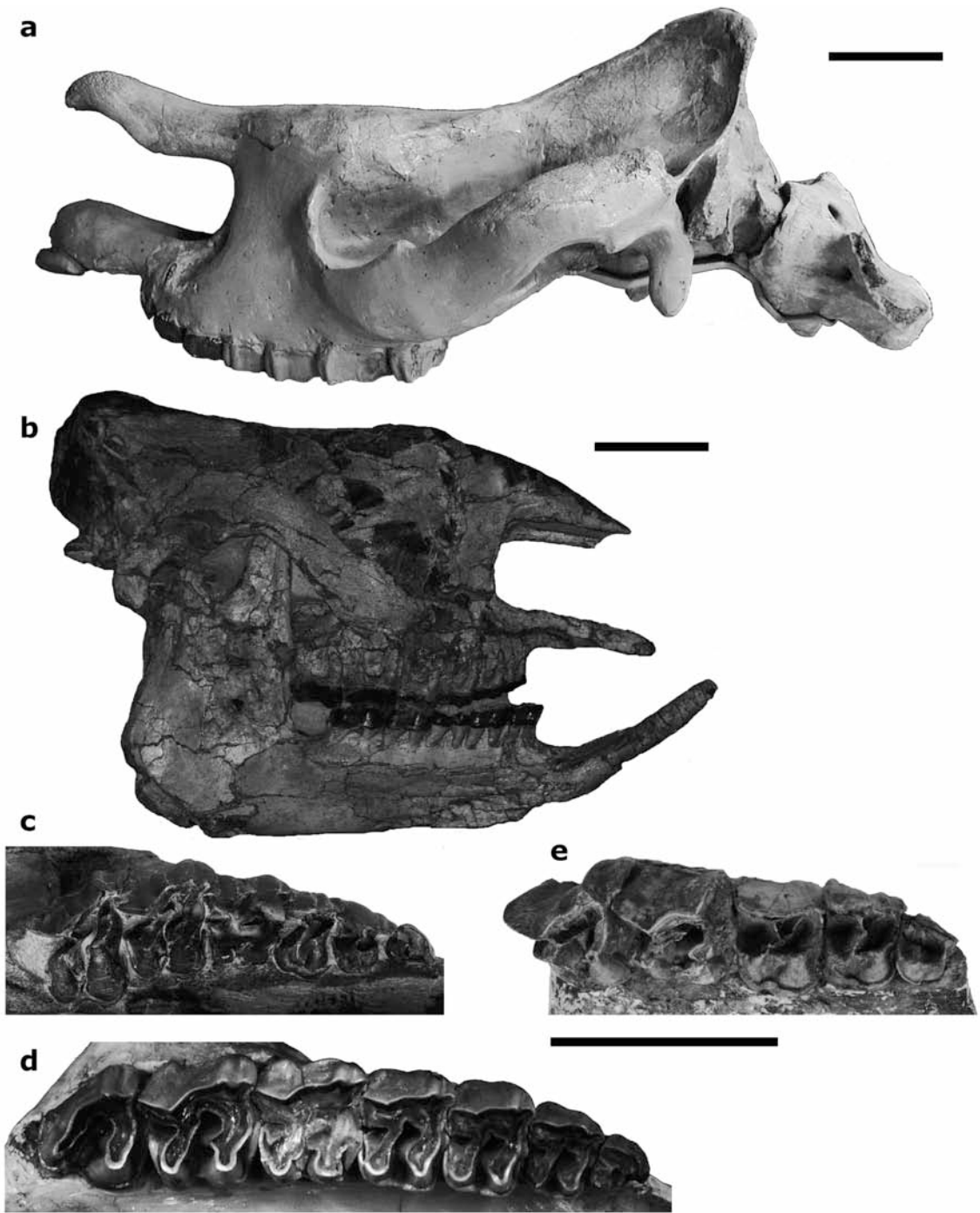


Fig. 4. Skulls and upper tooththrows of European Aquitanian *Diaceratherium*. **a:** skull (NMB–Sau1662) of *Diaceratherium asphaltense* (DEPÉRET & DOUXAMI, 1902) from the Aquitanian of Saulcet (Allier, France), left lateral view; **b:** skull (NMBE–D3193) of *Diaceratherium cf. lemanense* (POMEL, 1853) from the Auitanian of Engehalde (Bern, Switzerland), right lateral view; **c:** upper right tooththrow (D1–P2–3–D4–M1–2) from the skull (NMSG–P2006/1) of *Diaceratherium lemanense* (POMEL, 1853) from the Aquitanian of Eschenbach (St. Gallen, Switzerland), occlusal view; **d:** upper right tooththrow (P1–M3) from the skull (NMB–SAU1662) of *Diaceratherium asphaltense* (DEPÉRET & DOUXAMI, 1902) from the Aquitanian of Saulcet (Allier, France), occlusal view; **e:** upper right tooththrow (P2–M2) from the maxilla (MGL–3356) of *Diaceratherium aginense* (RÉPELIN, 1917) from the Aquitanian of Béthusy (Vaud, Switzerland), occlusal view. Scale bars: 10 cm.

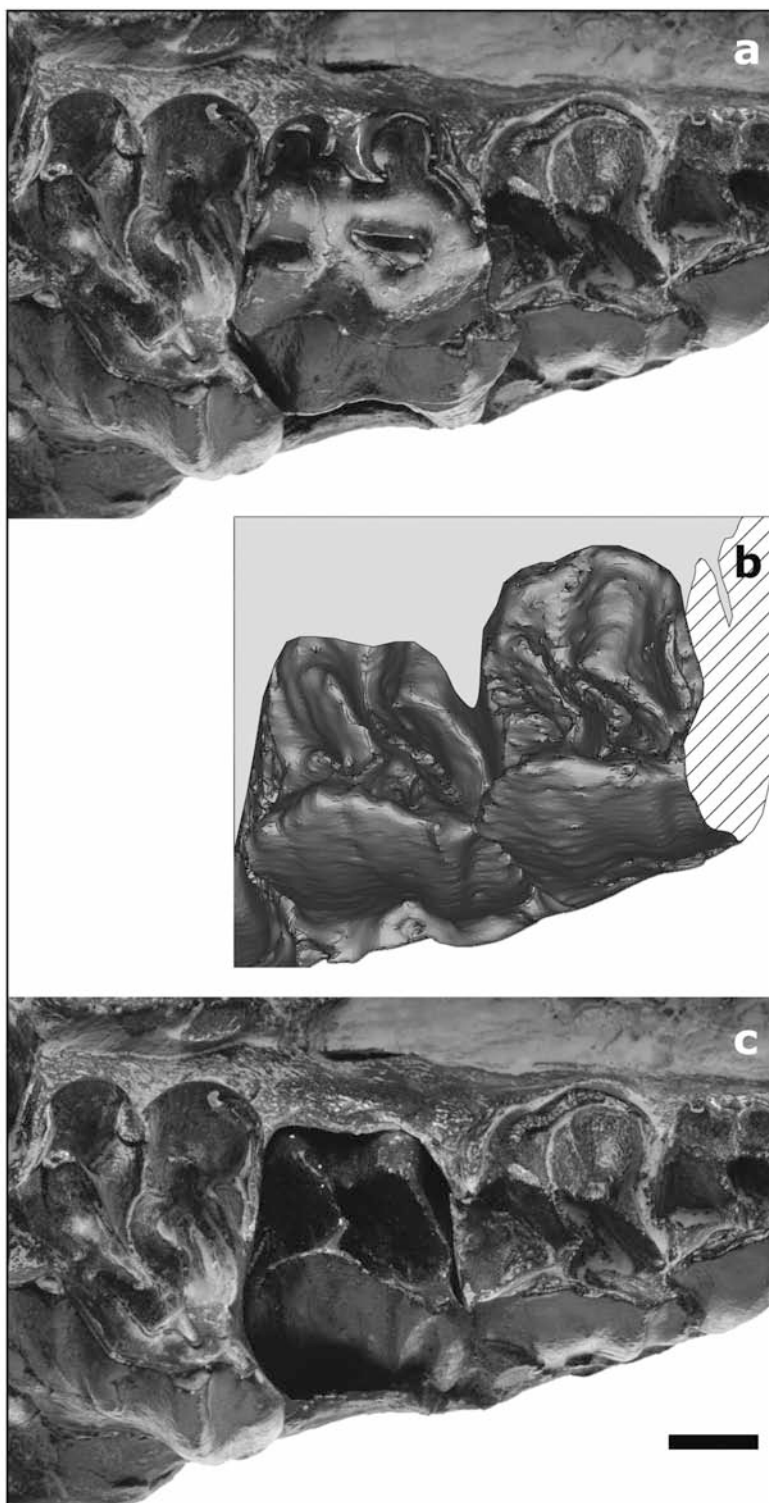


Fig. 5. *Diaceratherium lemanense* (POMEL, 1853), Eschenbach (St. Gallen, Switzerland), Aquitanian; **a**, P3-D4 cast of the skull NMSG–P2006/1, occlusal view; **b**, P3-4 digitized from computed tomography data of the skull NMSG–P2006/1, occlusal view; **c**, P3-4 cast from the computed tomography data of the skull NMSG–P2006/1. Scale bar: 1 cm.

Upper molars. The M1 and M2 are subquadrangular. The crochet is always well developed and the crista only slightly marked on the M1. The antecrochet is thick on the M1, but is weakly developed in depth on

the M2. The ectoloph profile is strongly oblique with respect to the axis of the toothrow, wing shaped in its posterior edge (in particular on the M2). The paracone folding is bulging, the parastyle and metastyle are

Table 7. Biometrical dimensions and hypsodonty index of the upper back teeth of the *Diaceratherium* species. The data in italics are from the literature.

Tooth dimensions		<i>D. lamilloquense</i> La Milloque MICHEL 1983	<i>D. aff. Lemanense</i> Paulhiac BRUNET et al. 1987	<i>D. lemanense</i> Cindré ROMAN 1911	<i>D. lemanense</i> Eschenbach NMSG– P2006/1	<i>D. lemanense</i> St.-Gérand-le-Puy BRUNET et al. 1987	<i>D. asphalt-tense</i> Pyri-mont-Challonges UCBL– 212997	<i>D. asphalt-tense</i> Wischberg NMB– AS75	<i>D. asphalt-tense</i> Saulcet NMB-SAU 1662	<i>D. tomerdingense</i> Tomerdin gen DIETRICH 1931	<i>D. aginense</i> Béthusy MGL–3356	<i>D. aginense</i> Béthusy MGL–3356	<i>D. aureliana</i> Neuville-aux-Bois CERDEÑO 1993
		average	sin./dext.	sin./dext.	sin./dext.	average	sin./dext.	sin./dext.	sin./dext.	average	average	sin./dext.	average
I1	L	–	–	–	24.50/23.00	–	–	–	–/47.50	–	–	–	62.60
	W	–	–	–	11.50/11.00	–	–	–	–/18.50	–	–	–	25.75
	H	–	–	–	8.00/8.00	–	–	–	–/19.50	–	–	–	–
D1	L	–	–	21.00/–	21.00/22.00	–	–/24.00	–	24.50/25.00	25.00	–	–	24.20
	W	–	–	19.50/–	17.00/16.50	–	–/19.50	–	21.50/23.50	–	–	–	18.60
	H	–	–	–	–	–	–/13.00	–	16.50/17.50	–	–	–	–
	I-Hy	–	–	–	–	–	–/54.17	–	67.35/70.00	–	–	–	–
P2	L	28.13	28.0	25.50/–	(28.00/28.00)	32.00	31.50/29.00	–	29.50/32.50	31.00	31.50	(26.00)/29.50	30.65
	W	36.87	41.0	31.00/–	(33.50/31.00)	40.00	34.50/34.00	–	37.50/39.00	31.00	41.33	35.50/(31.00)	37.63
	H	–	–	–	26.00/30.50	–	20.00/19.50	–	24.00/23.50	33.00	–	–	–
	I-Hy	–	–	–	92.86/108.93	–	63.49/67.24	–	81.36/72.31	106.45	–	–	–
P3	L	32.00	33.0	32.00/–	(29.50/28.50)	35.00	34.50/34.00	–	36.50/35.50	34.00	38.16	(42.50)/38.50	34.10
	W	41.13	50.0	39.50/–	39.50/36.50	50.00	46.00/45.00	–	47.00/47.50	42.00	51.50	50.00/46.00	45.24
	H	–	–	–	31.00/29.00	–	23.00/25.50	–	24.00/26.50	35.00	–	41.00/41.00	–
	I-Hy	–	–	–	105.08/101.75	–	66.67/75.00	–	65.75/74.65	102.94	–	96.47/106.49	–
D4	L	–	–	–	(36.00/36.00)	–	–	–	–	42.50	–	–	46.90
	W	–	–	–	39.50/39.00	–	–	–	–	40.00	–	–	43.10
	H	–	–	–	–	–	–	–	–	33.00	–	–	–
	I-Hy	–	–	–	–	–	–	–	–	76.65	–	–	–
P4	L	33.63	34.50	33.50/–	(30.00/–)	36.50	39.50/40.00	–	–/37.00	35.00	40.50	42.50/40.50	41.50
	W	47.13	51.50	–	(32.00/–)	54.75	50.00/52.00	–	–/49.50	47.00	56.33	49.00/53.00	52.73
	H	–	–	–	–	–	27.00/28.00	–	–/27.00	42.00	–	48.00/47.50	–
	I-Hy	–	–	–	–	–	68.35/70.00	–	–/72.97	120.00	–	112.94/117.28	–
M1	L	46.00	–	42.00/–	(39.50/40.50)	42.00	47.50/47.50	38.00/–	–/48.00	46.50	48.16	–/–	50.67
	W	49.00	–	52.00/–	51.00/51.50	56.00	52.50/52.00	50.50/–	–/52.00	46.00	59.25	–/49.50	51.08
	H	–	–	–	39.00/41.00	–	28.00/29.00	–	–/23.50	42.00	–	–/45.00	–
	I-Hy	–	–	–	98.73/101.23	–	58.95/61.05	–	–/48.96	90.32	–	–	–
M2	L	48.50	–	46.00/–	(45.00/43.50)	45.50	51.50/52.50	48.50/–	–/51.50	51.50	53.16	58.00/59.50	56.85
	W	54.00	–	52.50/–	57.00/54.50	58.50	56.50/55.50	53.00/–	–/55.00	51.00	59.83	55.50/54.50	59.80
	H	–	–	–	39.00/43.50	–	34.00/34.50	–	–/31.00	(42.00)	–	44.00/43.00	–
	I-Hy	–	–	–	86.67/100.00	–	66.02/65.71	–	–/60.19	81.55	–	–	–
M3	L	–	–	56.50/–	(42.00/–)	–	57.00/56.50	59.50/–	–/55.50	–	–	–	54.58
	abs	–	–	–	–	–	–	–	–	–	–	–	–
	L	43.00	–	46.00/–	(36.00/–)	–	44.00/45.50	49.00/–	–/43.50	–	–	–	46.65
	anat	–	–	–	–	–	–	–	–	–	–	–	–
	W	52.75	–	49.50/–	(43.50/–)	–	49.00/52.00	50.50/–	–/51.00	–	–	–	52.37
L	H	–	–	–	–	–	36.00/37.00	–	–/31.00	–	–	–	–
	I-Hy	–	–	–	–	–	81.82/81.32	–	–/55.86	–	–	–	–
L TR		–	–	225.00	(190.00)/–	–	234.0/250.0	–	–/255.00	–	(242.5)	–	–
L P		–	–	110.00	101.50/95.50	–	102.0/120.0	–	125.0/127.5	–	(117.0)	–	–
L P3-P4		–	–	68.00	58.50/56.00	–	72.00/74.00	–	73.00/72.00	–	(75.0)	–	71.00
L M		–	–	124.00	(116.00)/–	–	138.0/140.0	133.00/–	–/140.00	–	(160.0)	–	129.00

strongly elongated, and the mesostyle and metacone folding are very weakly marked. As on the premolars, the metaloph is oblique forming an angle at the starting of crochets when the protoloph and metaloph are parallel. The protocone constriction is well marked on the M1 but weaker on the M2, where it is only marked on the anterior face of the protoloph. The anterior face of the metaloph of the molars M1 and M2 is also constricted and the median valleys are deep, S-shaped and closed by secondary tubercles.

The postfossette shows the same depth than the median valley. The lingual cingulum is absent and a labial cingulum is only weakly marked at the base of the metacone folding on the M1.

4.2. Tomography analyses, modelling and rapid prototyping (Fig. 5)

The P4 digitized picture and cast are characterised by a quadrangular outline and a rather flat ectoloph with

a marked paracone folding. Like the P3, the P4 cast is semi-molariform to molariform showing a weak and low lingual bridge between the protocone and the hypocone, fused crista and crochet in depth delimiting a pseudo-medifossette, a S-shaped median valley, and deep postfossette and median valley. The M3 digitized picture and cast show a triangular shape, a bulging paracone folding, a well-marked crochet and a less-developed antecrochet.

4.3. Palaeobiogeographical maps (Tab. 8, Fig. 6)

The 178 large mammal localities are divided into 6 time intervals from MP29 to MN4, covering 7.4 million years (from 24.4 to 17.0 Ma). Each MP or MN biozone has 3 to 19 localities. During the latest Oligocene (MP29–30) the large mammal locality record seems weaker; it is mainly due to the lack of record in the Iberian Peninsula, but also because the MP29–30 time interval is very short. According to ENGESSER & MÖDDEN (1997), KEMPF et al. (1997) and SCHMIDT-KITTLER et al. (1997), the biochronostratigraphic resolution of the MP29–30 time interval is of 0.3 Ma per biozone. However, compared to the global record (MP29–MN4: nM/Ma = ca. 24), the distribution per million years is over the general mean. During the early Miocene (MN1–4), the distribution per million years is never less than 12. The number of localities dated to MN1 is relatively weak in Switzerland, because of a general uplift in the distal part of the Molasse Basin (sedimentary gap of the Jura Molasse) and the Alpine thrust of the proximal part (Subalpine Molasse) due to the Alpine orogenesis (BERGER et al. 2005); in MN3 and in MN4 a lower peak (nM/Ma = 12.4) and a higher peak (nM/Ma = 64) can be observed. These anomalies, strongly marked in Switzerland and Germany, are probably controlled by the transgressive-regressive phase of the perialpine Burdigalian Sea from south-western France to the Swiss Molasse Basin (OMM = *Obere Meeresmolasse* = Upper Marine Molasse, MN2b–4; BERGER et al. 2005).

The richness of the Iberian Peninsula large mammal localities is particularly high in MN4 (nM/Ma = 32), whereas no localities are recorded during the MP29–MN1 interval. The depositional systems in the internal basins of the Iberian block remain remarkably constant throughout the Tertiary. The sedimentary record of the Pyrenees and its bordering areas indicate that marine and subsequent fluvio-lacustrine sedimentation in the Pyrenean foreland basins stop-

Table 8. Distribution of large mammal localities per biozone (nM), per million years (nM/Ma), and commonness (locality coverage) of *Diaceratherium* localities (%D.) in Western Europe. MB = Mammal Biozones, TI = Time Interval in millions of years, IP = Iberian Peninsula, FR = France, SW = Switzerland, GE = Germany, WE = Western Europe.

MB		MP29	MP30	MN1	MN2	MN3	MN4	MP29-MN4
TI		0.3	0.3	1.3	2.0	2.5	1.0	7.4
IP	nM	–	–	–	8	9	32	49
	nM/Ma	–	–	–	4.00	3.60	32.00	6.62
	%D.	–	–	–	12.50	22.22	3.13	8.16
FR	nM	5	4	9	8	15	17	58
	nM/Ma	16.67	13.33	6.92	4.00	6.00	17.00	7.84
	%D.	20.00	25.00	77.77	62.50	80.00	11.76	48.28
SW	nM	4	2	4	16	6	3	35
	nM/Ma	13.33	6.67	3.08	8.00	2.40	3.00	4.73
	%D.	0	0	50.00	62.50	50.00	0	42.86
GE	nM	1	2	8	12	1	12	36
	nM/Ma	3.33	6.67	6.15	6.00	0.40	12.00	4.86
	%D.	0	50.00	50.00	25.00	100	8.33	27.78
WE	nM	10	8	21	44	31	64	178
	nM/Ma	33.33	26.67	16.15	22.00	12.40	64.00	24.05
	%D.	10.00	25.00	61.90	43.18	58.06	6.25	32.02

ped around the Eocene–Oligocene transition, but also during the middle Miocene (MEULENKAMP & SISSINGH 2003). These geological aspects could partially explain that the Iberian large mammal locality distribution during the Oligo–Miocene transition is recorded only since MN2 and is maximal in MN4.

The mean *Diaceratherium* commonness is rather high (%D. > 30%), in particular during the MN1–MN3 interval (%D. > 50%). The weaker commonness during the MP29–30 interval is significant as well as the drastic decrease during MN4, because no sampling effects are detected into the Western European locality distribution. The occurrence of *D. cf. aurelianense* described in Loranca at the end of the MN2 biozone (CERDEÑO 1992, CERDEÑO & NIETO 1995) is assumed to be the FAD of the Spanish *Diaceratherium*, due to the very weak *Diaceratherium* commonness with respect to other countries such as France or Switzerland, whereas the large mammal locality distribution is in the Western Europe average. Moreover, the lack of *Diaceratherium* localities into the MP29–MN1 interval from the Iberian Peninsula has probably no influence on the European *Diaceratherium* commonness, because it does not count any large mammal localities. Finally, the disappearance of the diaceratheres just after the “Proboscidean Datum Event” is attested by the very high richness of the

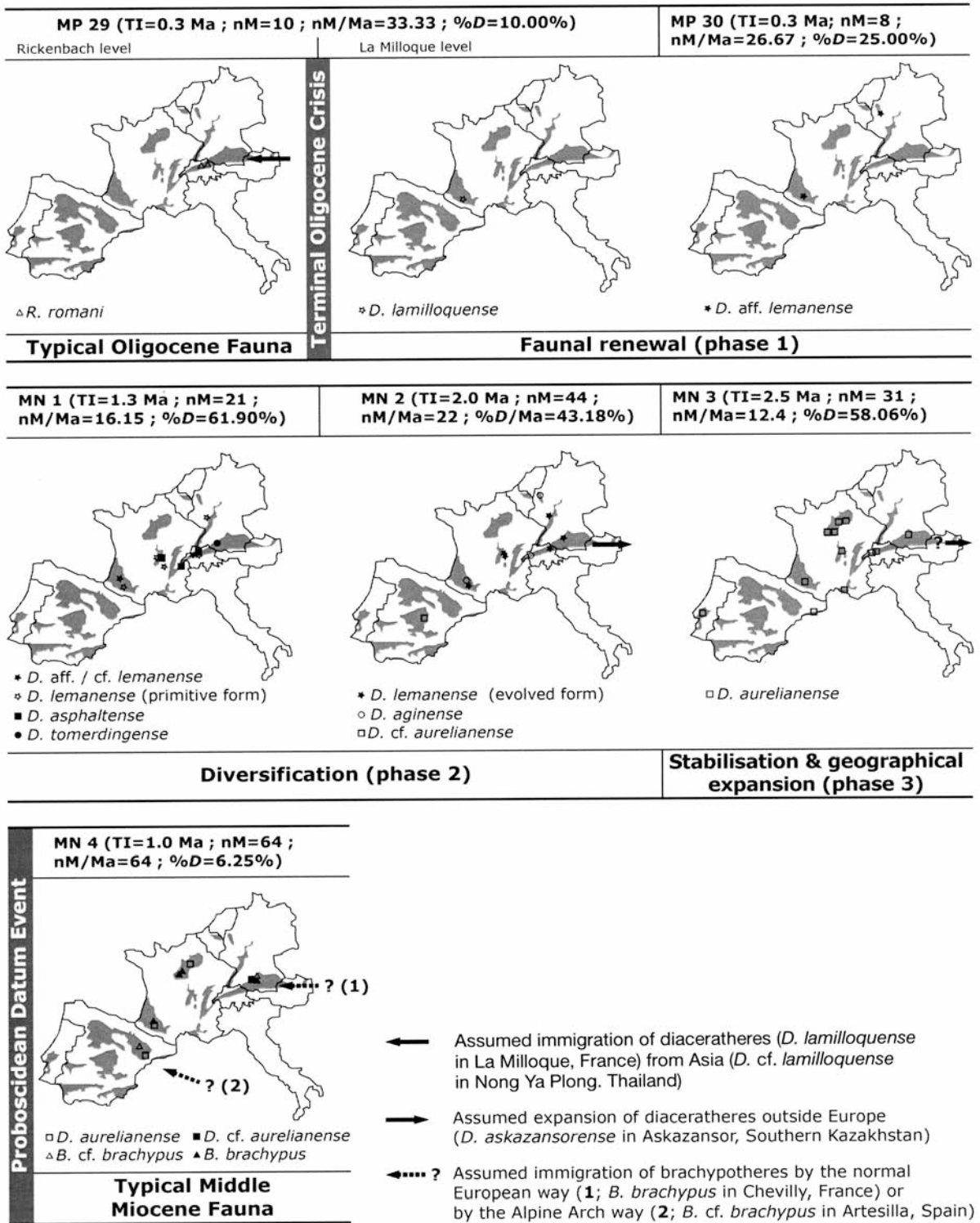


Fig. 6. Palaeobiogeographical distribution of the 57 European *Diaceratherium* localities (after the localities and the references reported in Table 3) compared with the last *Ronzotherium romani* and the first *Brachypotherium brachypus* localities. **TI**, time interval; **nM**, number of large mammal localities; **nM/Ma**, number of large mammal localities per million years; **%D**, commonness (locality coverage) of *Diaceratherium* localities. **Grey areas**, European Tertiary basins.

















Epoch	Early Oligocene	Late Oligocene		Early Miocene						Middle Miocene		
Biostrati.	MP22-24	MP25-29	MP30	MN1	a	MN2	b	MN3	a	MN4	b	MN5
Body size	medium-small			medium-small to medium-large								large
Body mass	medium-small			medium-small to medium-large	medium-large to large						large	
Slenderness	cursorial		mediportal	mediportal to graviportal				graviportal				
Metapod evolution	 <i>Ronzotherium filholi</i> Villebramar		 <i>Diaceratherium lamilloquense</i> La Milloque	 <i>D. aff. lemanense</i> Thézels	 <i>D. lemanense</i> (primitive form) Gannat	 <i>D. lemanense</i> (evolved form) Budenheim	 <i>D. asphaltense</i> Pyrimont-Challonges	 <i>D. aginense</i> Laugnac	 <i>D. aurelianense</i> Artenay	 <i>Brachypotherium brachypus</i> Chevilly	 10 cm	
Hypsodonty class	brachyodont		?	mesodont								
Feeding posture	specialized		?	specialized to indiscriminate				indiscriminate	indiscriminate (to specialized)			
Head holding evolution	 <i>Ronzotherium filholi</i> Villebramar		 <i>R. romani</i> Vendèze	 <i>D. lemanense</i> (pimitive form) Gannat	 <i>D. lemanense</i> (evolved form) Eschenbach	 <i>Brachypotherium</i> sp.			 20 cm			
Palaeoclim.	temperate		cold & dry	warm & dry	warm & wet			warm & wet with marked dry season				
Palaeoenv.	semi-open & humid		open & arid	rather open & rather arid	rather closed & rather humid		closed & humid	rather closed & rather humid				
Faunal evolution and bioevents	Typical Oligocene Fauna		Faunal renewal (phase 1)	Diversification (phase 2)			Stabilisa. & geogr. expansion (phase 3)	Typical Middle Miocene Fauna				

Fig. 7. Evolution of the palaeoecological parameters of the *Diaceratherium* species, compared with *Ronzotherium filholi*, *R. romani* and *Brachypotherium brachypus* (after the data reported in Tables 9 and 10). The fossil drawings are modified after NOUËL 1866 (skull of *Diaceratherium aurelianense*, Neuville-aux-Bois), DÉPÉRET & DOUXAMI 1902 (McIII and skull of *Diaceratherium asphaltense*, Pyrimont-Challonges), ROMAN 1911 (skull of *Diaceratherium lemanense*, Gannat), ROMAN 1924 (McIII of *Diaceratherium lemanense*, Budenheim), RÉPELIN 1917 (skull of *Diaceratherium aginense*, Laugnac), DIETRICH 1931 (McII of *Diaceratherium tomerdingense*, Tomerdingen), DE BONIS 1973 (McIII of *Diaceratherium aginense*, Laugnac), BRUNET 1979 (McIII and skull of *Ronzotherium filholi*, Villebramar; skull of *Ronzotherium romani*, Vendèze; McIII of *Diaceratherium lamilloquense*, La Milloque), MICHEL 1983 (McIII of *Diaceratherium aff. lemanense*, Thézels), PROTHERO et al. 1989 (skull of *Brachypotherium* sp.), CERDEÑO 1993 (McIII of *Diaceratherium aurelianense*, Artenay; McIII of *Brachypotherium brachypus*, Chevilly), BECKER 2003 (MtIII of *Ronzotherium romani*, Rickenbach) and unpublished photographs from the NMB (McIII of *Diaceratherium lemanense*, Gannat).

European large mammal locality distribution. For all these reasons the problematic issue of sampling is not

really critical for the most part of the considered time interval.

The overview of the Western European Oligo–Miocene palaeobiogeographical maps of the *Diaceratherium* localities underlines the latest Oligocene LAD of *Ronzotherium* (*R. romani* from Rickenbach and Rüfi bei Schänis in Switzerland; ENGESSER & MÖDDEN 1997, BECKER 2003) and the FAD of *Diaceratherium* (*D. lamilloquense* from La Milloque in France; BRUNET et al. 1987). The earliest Miocene is mainly characterised by the diversification of the *Diaceratherium* species (*D. lemanense*, *D. asphaltense*, *D. tomerdingense*, *D. aginense*). At the end of MN2, the FAD of *D. cf. aurelianense* occurs in the Iberian Peninsula, corresponding to the first occurrence of diaceratheres in this area. Into the MN3 biozone, there is no more than one *Diaceratherium* species (*D. aurelianense*), but it is also the time interval of the greater commonness and geographical extension of the diaceratheres in Western Europe. Finally, the LAD of diaceratheres (Eggingen-Mittelhart 3 in Germany; SACH & HEIZMANN 2001) and the FAD (Artesilla in Spain; CERDEÑO 1992, CERDEÑO & NIETO 1995) of the true brachypotheres in Europe mark the MN4 biozone pattern.

4.4. Palaeological parameters (Tabs. 9 and 10; Fig. 7)

The diacerathere palaeoecological parameters seem to follow the same pattern. We note ecological types close to ronzotheres within MP29–30, mixed ecological types within MN1–2 and close to brachypotheres within MN3–4.

Body size and mass. We can state a general pattern of increasing size and weight. Both parameters start with low values (compared to the early Miocene diaceratheres and brachypotheres) corresponding to *Ronzotherium* species and primitive diaceratheres of the latest Oligocene. During the early Miocene, particularly during the earliest Miocene (MN1–2), both parameters are mixed, regardless of the general increasing trend. From the late early Miocene the large sizes and forms become more and more exclusive.

Slenderness. This parameter, probably the more significant and characteristic, shows a progressive decreasing gracility. The ronzotheres are cursorial while the primitive diaceratheres are mediportal. The general pattern underlines mixed types within the earliest Miocene (mediportal to graviportal), but only the graviportal type exists since MN3.

Hypsodonty index and head holding. The crown height changes are only few marked. However, we can observe a slight progressive increase from brachyodont teeth (ronzotheres and primitive diaceratheres) to mesodont teeth (Miocene diaceratheres and brachypotheres). The head holding evolution is more changing. The ronzotheres belong to the low head holding type. The earliest Miocene diaceratheres show evidence of mixed head holdings (low and intermediate), whereas only the intermediate head holding is marked within MN3 by the last diacerathere representatives (*D. aurelianense*). The brachypotheres seems to show intermediate to low head holdings.

5. Discussion

5.1. Taxonomic affinities

Following GUÉRIN (1980) and CERDEÑO (1993), the Eschenbach specimen does not show the characteristics of the *Brachypotherium* genus, which generally presents larger dimensions, shorter nasals, broader postorbital constriction, as well as a lingual cingulum and a flat ectoloph profile (except a developed paracone folding) on the molars. The *Ronzotherium* genus also differs clearly from this specimen, showing an incomplete reduction of the anterior dentition (still composed of the I1 and I2) and a stronger occipital elevation (BRUNET 1979). Numerous morphological features of the Eschenbach skull (deep U-shaped nasal notch, long, fine and almost totally separated nasals, long and fine premaxilla, posterior elevation of the zygomatic arches) correspond to the descriptions of *Diaceratherium* skulls from the literature (POMEL 1853, DUVERNOY 1853, NOUEL 1866, DEPÉRET & DOUXAMI 1902, RÉPELIN 1917, DIETRICH 1931, LAVOCAT 1951, CERDEÑO 1993). The dental morphology (persistent D1, well marked parastylar groove on back teeth, strong lingual cingulum on premolars, developed antecrochet and crochet on molars, oblique and wing shaped ectoloph profile of the M1 and M2) is also typical for the *Diaceratherium* genus (DE BONIS 1973, MICHEL 1983, BRUNET et al. 1987, GINSBURG et al. 1981, 1991, CERDEÑO 1993, ENGESSER et al. 1993).

The dorsal profile of *D. aginense* and *D. aurelianense* skulls differs from that of the specimen from Eschenbach by a strong occipital elevation, a vertical occipital side, a tendency to the brachyocephaly, postglenoid and posttympanic apophyses rather separated, and broader zygomatic arches (NOUEL 1866, ROMAN 1911, RÉPELIN 1917, CERDEÑO 1993). The *D. as-*

Table 9. Ecological data of *Ronzotherium*, *Diaceratherium*, *Brachypotherium* and living rhinoceroses, based on tooth and bone biometry and description. The *body masses are not based on the method of LEGENDRE (1989), but on the correlation regression of body mass on skull length (occipital condyles-premaxilla). *D.* = *Diacerathium*, *B.* = *Brachypotherium*, *R.* = *Rhinoceros*, *C.* = *Ceratotherium*.

Taxon	Locality	Data sources of osteologic and dentary material	Body mass	TDT (mm)	I-Gr (McII)	I-Gr (McIII)	I-Gr (MtIII)	I-Hy	Head posture
<i>Ronzotherium filholi</i>	Villebramar Bumbach	Brunet 1979, Emery 2004, direct observation Becker 2003	*1075 kg –	54.00 –	20.45 26.10	20.40 –	– –	64.0 82.1	down –
<i>Ronzotherium romani</i>	Vendéze Rickenbach	Brunet 1979 Becker 2003, Emery 2004, Emery et al. 2007, direct observation	*780 kg –	– 51.00	– –	– –	– 23.65	– 63.5	down –
<i>Diaceratherium lumilloquense</i>	La Milloque	Michel 1983	1043 kg	–	–	28.10	–	–	–
<i>Diaceratherium aff. lemanense</i>	Thézels Paulhiac	Michel 1983 Michel 1983	1375 kg 1342 kg	60.00 52.75	– –	28.05 29.60	– –	– –	– –
<i>Diaceratherium cf. lemanense</i>	Engelhalde	direct observation	1202 kg	–	–	–	–	–	down
<i>Diaceratherium lemanense</i>	Gannat (prim. form) Wischberg Eschenbach (ev. form) Budenheim (ev. form)	Roman 1911, Michel 1983, direct observation direct observation direct observation Roman 1924	– 1430 kg – –	63.50 54.50 – 54.00	– – – –	– – – 29.93	30.40 – – 27.78	– – 108.93 –	down (-intermediate) – down –
<i>Diaceratherium asphaltense</i>	Pyrimont-Challonges Saulcet Wischberg	Depéret & Douxami 1902, direct observation direct observation direct observation	1779 kg – 1790 kg	– – 61.00	25.50 – –	33.10 – –	31.90 – –	81.32 74.65 –	intermediate intermediate intermediate
<i>Diaceratherium tomerdingense</i>	Tomerdingen 2	Dietrich 1931	1779 kg	–	34.80	–	–	120.00	–
<i>Diaceratherium aginense</i>	Bethusy Moulin d'Assens Laugnac	Engesser et al. 1993 Engesser et al. 1993 Repin 1917, de Bonis 1973, Michel 1983	2141 kg 2278 kg 1689 kg	– – 54.00	– – 31.00	– – 32.75	– – –	117.28 – –	– – intermediate
<i>Diaceratherium aurelianense</i>	Brüttelen 1 Cheyres Pra Bosset Beaulieu Moli Calopa Neuville-aux-Bois Chilleurs-aux-Bois Artenay	Becker 2003 Becker 2003 Aguilar et al. 2003 Santafe Llopsi 1978 Noel 1866, Mayer 1908, Cerdeño 1993 Cerdeño 1993 Cerdeño 1993	– – 1712 kg – 1531 kg 1665 kg 1712 kg	51.50 – 55.80 – 50.30 48.00 56.70	– – – – 30.76 29.47 33.10	– – – – 34.73 – 36.60	– – – – 36.44 – 41.03	– 80.15 – 80.41 – – –	– – – – intermediate (-up) – –
<i>Brachypotherium brachypus</i>	Chevilly Baigneaux Beaugency La Romieu Savigné Pontlevoy Malartic Montchaibeux	Cerdeño 1993 Cerdeño 1993 Cerdeño 1993 Cerdeño 1993 Cerdeño 1993 Cerdeño 1993 Cerdeño 1993 Becker 2003	– – 2767 kg 2155 kg – 2333 kg 2490 kg –	73.95 70.00 – 73.00 67.60 68.00 74.45 62.50	– – – 24.74 – – 30.86 –	37.88 32.10 – 29.71 – – 36.75 –	– – – 34.65 – – 38.75 –	– – – – – – – –	– – – – – intermediate (-down) – intermediate
<i>Brachypotherium perimense</i>	Nikkiwalanala (PK)	Heissig 1972	–	–	–	–	38.02	–	intermediate
<i>Brachypotherium sp.</i>	– –	Guérin 1980 Prothero et al. 1989	– –	– –	– –	– –	– –	97.25 –	– intermediate
<i>Ceratotherium simum</i>	–	Guérin 1980	2423 kg	64.85	23.15	30.01	28.03	195.32	down
<i>Diceros bicornis</i>	–	Guérin 1980	*1075 kg	62.05	23.82	28.0	27.07	139.18	intermediate
<i>Rhinoceros unicornis</i>	–	Guérin 1980	2166 kg	75.00	23.07	28.21	27.34	130.29	up
<i>Rhinoceros sondaicus</i>	–	Guérin 1980	1810 kg	61.20	26.28	33.63	34.67	115.17	up
<i>Dicerorhinus sumatrensis</i>	–	Guérin 1980	1190 kg	55.30	23.98	27.03	26.78	120.82	intermediate

phaltense skull shows a higher occipital crest, a rather vertical occipital side, separated postglenoid and posttympanic apophyses, and significantly broader zygomatic arches (DEPÉRET & DOUXAMI 1902). In

addition, its nasal tip is slightly elevated, forming a small convexity with a double lateral rough tubercle, separated by unfused nasals. These bumps are particularly well marked on the skulls of the specimens

Table 10. Overview of the different ecological parameters of *Ronzotherium*, *Diaceratherium*, *Brachypotherium* and living rhinoceroses (after BALES 1996, NOWAK 1999, CHRISTIANSEN 2002, <http://animaldiversity.ummz.umich.edu/site/index.html>, <http://www.rhinos-irf.org>; see also Tab. 9 for data sources of osteological and dental material). The * body mass parameters are not supported by method of LEGENDRE (1989), but by the correlation regression of body mass on skull length (occipital condyles-premaxilla).

Taxon	Body mass from literature (kg)	Body mass from the method of Legendre 1989	Shoulder height from literature (cm)	Body size based on the TDT	Slenderness based on the I-Gr	Dietary regime and hypsodonty class	Feeding behaviour based on head holding (= feeding posture)	Diet and environment based on extant rhinoceroses
1 <i>Rhinoceros unicornis</i>	1800-2700	large	180-200	large	mediportal	GrBr-H	specialized in tall vegetation	mixed feeder living in floodplain with open high-grassland, bushland, swamp and river areas
2 <i>Ceratotherium simum</i>	1800-2700	large	150-180	medium-large	graviportal	Gr-H	specialized in short vegetation	roughage and dry region grazer living in flat open grassland with isolated trees
3 <i>Rhinoceros sondaicus</i>	900-2300	medium-large	150-170	medium-large	graviportal	Br-M	specialized in tall vegetation	high browser living in dense to slightly open forest close to water beds or swamps
<i>Brachypotherium brachypus</i>	–	large	–	medium-large to large	graviportal	Br-M	indiscriminate (to possibly specialized in short vegetation)	
<i>Diaceratherium anrehanense</i>	–	medium-large	–	medium-small	graviportal	Br-M	indiscriminate (to possibly in tall vegetation)	
<i>Diaceratherium aginense</i>	–	large	–	medium-small	graviportal	Br-M	indiscriminate (to specialized in tall vegetation)	
<i>Diaceratherium asphaltense</i>	–	medium-large	–	medium-large	graviportal	Br-M	indiscriminate	
<i>Diaceratherium tomerdingense</i>	–	medium-large	–	–	graviportal	Br-M	–	
4 <i>Diceros bicornis</i>	800-1400	*small to medium-small	140-170	medium-large	mediportal	Br-H	indiscriminate	regular browser living in bushland, in the transitional zone between forest and grassland
<i>D. lemanense</i> (evolved form)	–	medium-small	–	medium-small	mediportal	Br-M	possibly specialized in short vegetation	
<i>D. lemanense</i> (primitive form)	–	medium-small	–	medium-large	mediportal	Br-?	possibly specialized in short vegetation (to indiscriminate)	
5 <i>Dicerorhinus sumatrensis</i>	600-950	medium-small	100-150	medium-small	mediportal	Br-H	indiscriminate	regular browser living in rainforest close to water beds or swamps
<i>Diaceratherium lamilloquense</i>	–	medium-small	–	–	mediportal	Br-?	–	
6 <i>Ronzotherium romani</i>	–	*small	–	medium-small	cursorial	Br-B	possibly specialized in short vegetation	regular browser living in open woodland
<i>Ronzotherium filholi</i>	–	*small to medium-small	–	medium-small	cursorial	Br-B	possibly specialized in short vegetation	

from Saulcet (NMB–Saul662; Fig. 4a), Wischberg (NMB–AS75; SCHAUB & HÜRZELER 1948) and Pyrimont-Challonge (UCBL–212997; DEPÉRET & DOUXAMI 1902). In fact, as suggested by CERDEÑO (1995), the development of nasal horns evolved independently to apomorphic states and with sometimes reversals to the plesiomorphic state (absence). Thus, the occurrence of paired nasal horns in *D. asphaltense* is rather interpreted as a convergence with that in *Diaceratherium*, *Menoceras* and *Pleuroceros*. However, DE BONIS (1973) excludes the existence of a double nasal horn for *D. asphaltense* from Pyrimont-Challonge, because the lateral rough bumps are too weak. He notes also that the young forms of extant rhino-

ceroses with a unique nasal horn show commonly symmetric rough bumps on the nasal tip getting larger and fused with years. Additionally, the development, the presence and the absence of horns can often be linked to sexual dimorphism (ANTOINE 2002, PROTHERO 2005). For all these reasons, the “horn” in the Rhinocerotidae is not a “good” diagnostic character (ANTOINE, pers. comm.). In this way, we cannot exclude that the lack of horn in the Eschenbach specimen is a consequence of the juvenile state, the sexual dimorphism or a reversal to the plesiomorphic state, even so no horned skull of *D. lemanense* is mentioned in the literature, except LAVOCAT (1951) who considers *D. lemanense* and *D. aginense* as syno-

nymys. Nevertheless, numerous authors report the presence of nasal horn in *Diaceratherium* species in addition to the *D. asphaltense* (*D. aurelianense* from Artenay, Neuville-aux-Bois, Chilleurs-aux-Bois, NOUEL 1866 and CERDEÑO 1993; *D. aginense* from Laugnac, RÉPELIN 1917 and DE BONIS 1973; *D. tomerdingense* from Tomerdingen, DIETRICH 1931).

The main characters of the Eschenbach skull (long and fine nasals, deep U-shaped nasal notch reaching the middle of the P3, postglenoid and posttympanic apophyses in contact, slight posterior elevation and enlargement of the zygomatic arch, weakly separated sagittal crests, slight dome on the nasal posterior edge, occipital side inclined backward) are very close to those of the *Diaceratherium lemanense* from Gannat, illustrated by ROMAN (1911: Pl. VIII, fig. 1 and 1a). However, the Eschenbach skull exhibits a slight flexure of the zygomatic arch in its posterior half, indicating probably a more evolved state. This character is associated with a lateral enlargement in *D. asphaltense* and *D. aurelianense*, while the zygomatic arch of *D. aginense* is rectilinear while elevated and broad.

The skull from Engehalde (NMBE–D3193; Fig. 4b) ascribed to *Acerotherium gannatense* by OOSTER & von FISCHER-OOSTER (1871; Pl. 1 and 2) is fairly different, displaying an elevated and strongly curved zygomatic arch, a high and robust nasal, and a high skull in lateral view. But these characters seem to be artefacts due to a transverse flatness of the skull which have elevated the arches, narrowed the orbito-temporal opening and curved the nasals. Moreover, it is impossible to observe the occlusal view of the back teeth on this skull. For all these reasons, we ascribe this material to *Diaceratherium* cf. *lemanense*.

The dental structures of the Eschenbach skull exhibit some evolved features (crista and crochet developed and fused on premolars, very marked posterior wing shape of ectoloph in the M1 and M2, strongly-developed crochet on molars, triangular M3), which are present in *D. aginense* (e.g. *D. aginense* from Laugnac, RÉPELIN 1917; *D. aginense* from Béthusy, MGL–3356, Fig. 4e; ENGESSER et al. 1993) and in the evolved *D. lemanense* from Saint-Gérard-le-Puy (BRUNET et al. 1987). However, the dental biometrical data of *D. aginense* are systematically larger, quite as those of the specimen from Saint-Gérard-le-Puy (Tab. 8). Of course, the Eschenbach skull belongs to a juvenile specimen and could be a female as well.

In comparison, the tooththrow of *D. lemanense* from Cindré, illustrated by ROMAN (1911; Pl. VIII, fig. 2a), seems more primitive, exhibiting a slightly subquadratic M3, a posterior wing-shaped ectoloph less marked on M1 and M2, and a crochet poorly developed in the molars. The back tooth structure of *D. asphaltense* is also quite different with mainly molariform premolars, a subquadratic M3, a weakly developed or absent crochet on the molars, and a less-marked posterior wing-shaped ectoloph on M1 and M2 (e.g. *D. asphaltense* from Saulcet, NMB–Sau1662, Fig. 4d; *D. asphaltense* from Pyrimont-Challonges, UCBL–212997, DEPÉRET & DOUXAMI 1902). Concerning the enigmatic *D. tomerdingense* of DIETRICH (1931), the differences are obvious: larger size (Tab. 8), no parallelism between the protoloph and the metaloph of the P3, no antecrochet on molars. Moreover, the metapods of *D. tomerdingense* are indisputably stouter in comparison with those of *D. lemanense* from Gannat exhibited in the NMB (pers. obs.). As noted by MICHEL (1983) in order to distinct *D. lamilloquense* from *D. lemanense*, the former differs from the Eschenbach specimen by a larger L/W ratio of the back teeth and more primitive dental characters (less advanced molarisation of the premolars and less developed antecrochet on molars). As there is no comparison material of *D. cf. lemanense* from Thézels, we consider, following MICHEL (1983) and BRUNET et al. (1987), that the latter is more evolved than *D. lamilloquense* and more primitive than *D. lemanense*. Finally, the dental series of the Eschenbach specimen are too primitive to belong to *D. aurelianense*, which presents molariform premolars, very strong paracone folding and well-developed crochet, crista and antecrochet on molars (GINSBURG et al. 1981, CERDEÑO 1993).

The set of morphological features on the Eschenbach skull and the comparison with other European specimens ascribe it to *Diaceratherium lemanense* (POMEL 1853). It is probably in a more evolved state than the Gannat specimen and although its dental structures are closer to those of the Saint-Gérard-le-Puy specimen, it shows certainly a more primitive state than the latter.

5.2. Ontogeny

The age of the Eschenbach specimen can be estimated from the dental formula of the back teeth – D1-P2-P3-D4-M1-M2 – and the computed tomography data. The latter allowed the description of the un-

erupted teeth P4 sin. and M3 sin., and also the growing state of the adult tooth eruption. According to GUÉRIN (1980), the eruptions of the P4 and the M3 are the two last steps prior to the adult state. The absence of an unerupted P1, as shown by the computed tomography, indicates a persistent D1. As discussed by PROTHERO et al. (1986) and PROTHERO (2005), the first deciduous premolars D1/d1 of most perissodactyls are never replaced but retained until adulthood or lost without a replacement tooth. This is even the prevailing condition in the Rhinocerotidae (BUTLER 1952). Consequently, the juvenile state of the specimen is not underlined by the retention of the D1, but above all by the non-eruption of the P4 and the M3. According to NOWAK (1999), the adult state of the closer living rhinoceros (*Diceros bicornis*) of *D. lemanense* is reached between 7 and 10 years. Assuming the same case in the fossil rhinocerotids, the Eschenbach specimen is probably between 5 and 7 years old.

5.3. Biostratigraphy (Fig. 8)

The first European occurrence of diaceratheres is the *D. lamilloquense* from La Milloque (France), in the Mammal Zone MP29 (BRUNET et al. 1987), just at the beginning of the “Terminal Oligocene Crisis”. During MN1 (earliest Miocene), this rhinocerotid group shows a relatively high diversity with three species (*D. lemanense*, *D. asphaltense* and *D. tomerdingense*), spreading from south-western France to eastern Switzerland and southern Germany. During MN2a, the *Diaceratherium* lineage is still represented by *D. lemanense*, but also by the first representatives of *D. aginense*. *Diaceratherium* cf. *aurelianense* appears during MN2b in Spain and is contemporaneous with the last *D. lemanense* and *D. aginense*. From MN3, only *D. aurelianense* persists, mainly in France, but also in the Iberian Peninsula, in Switzerland and in Germany. During MN4a, just after the “Proboscidean Datum Event”, the last occurrence of *D. aurelianense* is recorded in Artenay, France (GINSBURG 1989a, 1989b, CERDEÑO 1993), whereas the first occurrence of *Brachypotherium* is recorded in Artesilla (Spain) with *B. cf. brachypus* (AZANZA et al. 1993, CERDEÑO 1993). SACH & HEIZMANN (2001) note the occurrence of a *D. cf. aurelianense* in Germany (MN4b, Eggingen-Mittelhart 3).

Diaceratherium lemanense is widespread in the early Miocene of Germany, Switzerland and France, and appears to be the dominating species during MN1

(BRUNET et al. 1987, DURANTHON 1991, ANTOINE et al. 2006). According to the complete biostratigraphical record, this species is probably not restricted to the MN1 biozone, but ranges from MP30 with the primitive *D. aff. lemanense* from Thézels (COMTE 2000) and *D. lemanense* from Rott bei Bonn (VON KOENIGSWALD et al. 1992, MÖRS 2002) to MN2 with more evolved forms (Saint-Gérard-le-Puy and Montaigu-le-Blin, France, HUGUENEY 1997; Budenheim, Germany, ROMAN 1924). Consequently, the more evolved *D. lemanense* reported from Eschenbach is a new biostratigraphical pinpoint within the *Granitischer Sandstein* Formation. The taxonomical affinities assign it to the MN2a biozone. *Diaceratherium lemanense* Eschenbach is probably slightly younger than that from Cindré and slightly older than that from Saint-Gérard-le-Puy, but certainly older than *D. aginense* from Béthusy. In addition, the presence of *D. cf. lemanense* in Engehalde does not allow a more precise dating of this locality than the MN1–2 interval.

5.4. The Oligo–Miocene transition

Generally, the *Diaceratherium* lineage is characterised by mesodont back teeth, deep molar median valleys and fossettes, a deep nasal notch, mediportal to graviportal limbs and the retention of a fifth functional manus digit (DE BONIS 1973, MICHEL 1983, BRUNET et al. 1987). Within the large mammal herbivores, these features are interpreted as an aptitude to a slightly abrasive plant intake (FORTELIUS et al. 2002, 2003), as a presence of a useful prehensile lip to a feeding intake (GUÉRIN 1980, UHLIG 1999) – but normally coupled with retracted nasals after PROTHERO (2005) – and as a development of a certain amphibious way of life (CERDEÑO 1998, HEISSIG 1999). After CERDEÑO & NIETO (1995) and CERDEÑO (1998), the diaceratheres are associated to swampy habitats within woodland environments, where they live in relatively large groups like extant hippopotamuses. Their diet is composed of leaves and swampy short vegetation. However, these interpretations consider mainly the last species of the lineage (*D. aurelianense*). In fact, the diaceratheres are not necessarily associated to wetlands. For example, *D. tomerdingense* was found within a fissure filling located in the dry hinterland of lake environments from the USM in Baden-Württemberg (HEIZMANN, pers. comm.). Moreover, MIHLBACHLER (2005) argues that the shortened limbs of extinct hippo-like ungulates (in-

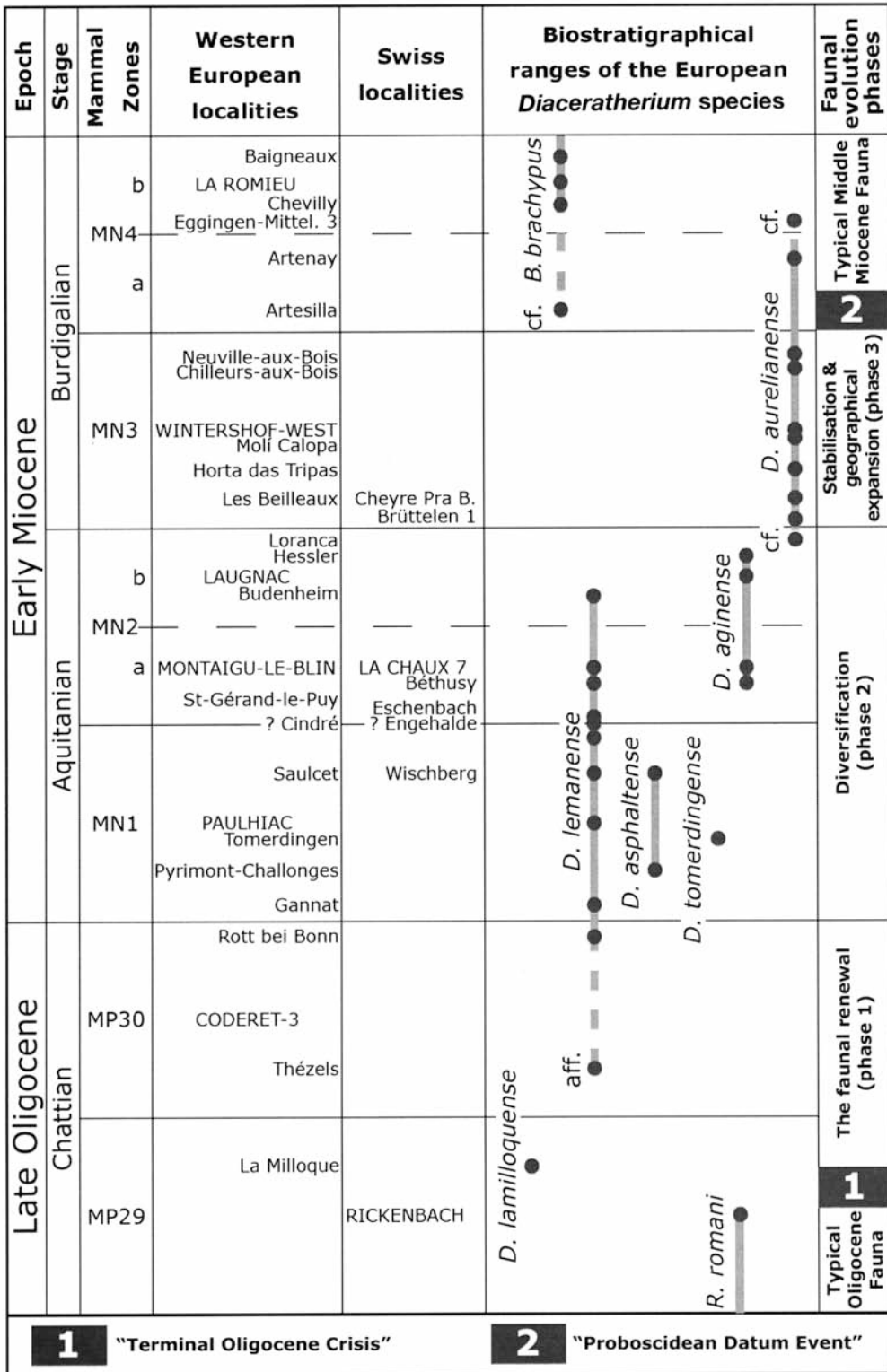


Fig. 8. Biostratigraphical ranges of the European *Diaceratherium* species compared with the LAD of *Ronzotherium romani* and the FAD of *Brachypotherium brachypus* in Western Europe (based on references in Table 3; SCHMIDT-KITTLER 1987, MEIN 1989, 1999, ENGESSER & MÖDDEN 1997, HEISSIG 1999).

cluding teleoceratines) are not clearly indicative of an aquatic lifestyle. An alternative hypothesis that the shortened limbs may have had more to do with open terrain and grazing habits is also possible. However, only few diaceratheres (*D. tomerdingense*, evolved *D. lemanense*, *D. aginense*) could be mixed feeders (browsers-grazers) in quite closed habitats (bushland, woodland or forest), but can never be true grazers.

The *Diaceratherium* genus is assumed to be a good representative of the Oligo–Miocene transition, from the “Terminal Oligocene Crisis” to the “Proboscidean Datum Event” (see Tab. 8: MP29–MN4 locality coverage, %*D.* > 30%). This time interval (MP29–MN4) is controlled by climatic and environmental changes and interaction phenomena (e.g. competition). The locality distribution patterns and the palaeoecological character evolution (e.g. body mass, feeding behaviour) of the *Diaceratherium* species seem to be a good proxy for understanding population fluctuations and pointing out climatic and environmental changes (especially during the MN1–3 interval). As it is illustrated in Figures 7 and 8, the Oligo–Miocene transition can be subdivided in three phases preceded by a “Typical Oligocene Fauna” and followed by a “Typical Middle Miocene Fauna”.

5.5. The typical Oligocene fauna

Late Oligocene (until Rickenbach level). A detailed environmental and climatic evolution of the Oligocene is beyond the scope of this study. Despite the cooling event in the mid-Oligocene (HAQ et al. 1987, PROTHERO 1994), the trend of an opening and a slight aridification of the environments in MP28 (COSTEUR 2005) and some significant faunal changes (see Introduction), we state that during the main part of the Oligocene the European climate was quite stable, generally marked by temperate conditions and several times partially associated with a vegetation of swamps and mangroves, as shown by REICHENBACHER et al. (2004) for the early Oligocene of the southern German Molasse. The late Oligocene records the FAD of *Diaceratherium* in Thailand with *D. cf. lamilloquense* (see MARIVAUX et al. 2004). This occurrence suggests an Asian origin for the European diaceratheres, as previously assumed by CERDEÑO (1998). The Rickenbach locality in Switzerland (European Reference Level for MP29) records the LAD of *Ronzotherium romani*. This species is a typical Oligocene cursorial regular browser, feeding on quite short vegetation and

inhabiting in dry open woodland. It has a relatively important size and weight compared to other contemporaneous mammals, but its weight is less important than in early Miocene diaceratheres. It disappears at the same time than *Anthracotheerium* and *Micobunodon*, prior to the “Terminal Oligocene Crisis”. The common *Ronzotherium-Anthracotheerium* association in the Oligocene European localities (e.g. Kleinblauen, Villebramar, La Ferté-Alais, Bumbach, Rickenbach) is typical for dry open woodlands associated with marshy forests (UHLIG 1999). EMERY et al. (2007) support an open and dry environment – maybe a scrub woodland type – for the Rickenbach mammal community. After TÖTKEN (pers. comm.), the enamel isotope composition from teeth of Rickenbach large mammals underlines a temperature peak probably analogous to the “Late Oligocene Warming” (cf. ZACHOS et al. 2001).

5.6. Faunal renewal (phase 1)

MP29 (from La Milloque level). This time interval coincides with the FAD of *Diaceratherium* in Europe – *D. lamilloquense* from La Milloque (France; BRUNET et al. 1987) – at the beginning of the “Terminal Oligocene Crisis”. This crisis is well documented in Switzerland by floral variations and important climatic changes, prior to the Oligocene/Miocene boundary (BERGER 1989, 1990a, 1990b): the presence of palms and taxads during the Oligocene shows a warm and humid climate, while their disappearance at the end of the Oligocene (at MP29) suggests a critical decrease of temperature and humidity. According to COSTEUR (2005), it seems to have some local and/or regional differences (e.g. the German localities of this biozone display more humid conditions). *Diaceratherium lamilloquense* exhibits a weak crown height and an early tendency to the brachypody, but does not yet reach the weight and the size of the Miocene diaceratheres (e.g. *D. aginense*, *D. aurelianense*). The drastic climatic and environmental changes, which generated drier and colder conditions, have probably forced this rather regular browser to inhabit refuge areas such as dense forests close to water sources. This is in agreement with the open and dry environments deduced by COSTEUR (2005) for the MP29–30 interval. Additionally – and contrary to ronzotheres which only have a reduced McV (BRUNET 1979) –, the diacerathere group is defined by the holding back of a fifth functional manus digit (MICHEL 1983, BRUNET et al. 1987). This feature

could be interpreted as an aptitude for living in swampy habitats or at least in humid wooded habitats with a moist and soft ground (DE BONIS 1973, HEISSIG 1999).

MP30. The diacerathere record of this biozone is restricted to *D. aff. lemanense* from Thézels (BRUNET et al. 1987) and *D. lemanense* from Rott bei Bonn (von KOENIGSWALD et al. 1992, Mörs 2002). The specimen from Thézels could represent the FAD of a primitive form of *D. lemanense*, probably derived from *D. lamilloquense*, from which it shows a closer anatomical type but with a slight increase of the crown height and body mass. It seems to be a regular browser inhabiting a different ecological niche, maybe in the transitional zone between forest and grassland, with available water. This could be related to the temporal vanishing of the forested refuge areas, associated with the opening of woodland habitats and an increasing seasonality.

5.7. Diversification (phase 2)

MN1. The diaceratheres are characterized by an increase of their diversity (*D. lemanense*, *D. asphaltense*, *D. tomerdingense*) and a first geographical spreading, from south-western France to eastern Switzerland and southern Germany. Some localities such as Saulcet (France) and Wischberg (Switzerland) could maybe also record two sympatric species (*D. lemanense* and *D. asphaltense*). The first representatives of a rather intermediate head holding are present with *D. asphaltense*, a probably rather high browser. The species of this time interval show an increase of the hypsodonty index, in particular *D. tomerdingense* (I-Hy = 120.00). However, the latter is only known in Tomerdingen in Germany and could represent a local speciation. Several anatomical types are represented – mediportal to graviportal types, medium-small to medium-large body masses and sizes –, characterising forms adapted to mosaic environments ranging from the dense or slightly open forests to the bushland. These observations are in agreement with those of BERGER (1989, 1990a, 1990b) and COSTEUR (2005) respectively based on floral changes and mammal community analyses. The general conditions remain open and dry, and the climate seems to support the bush and thorn-bush expansion. In western Switzerland the reappearance of palms – combined with the absence of Taxodiaceae and the diversification of Leguminosae – indicates an increase of the temperature coupled with low humidity. Furthermore,

COSTEUR (2005) assumes that environments are becoming scattered in mosaic form.

MN2. The FAD of the evolved *D. lemanense* (e.g. in Eschenbach; Fig. 9) and the possible speciation of *D. aginense* within MN2a of Switzerland (e.g. in Béthusy) highlight the second part of the diacerathere diversification. In fact, this earliest local occurrence of *D. aginense* in Switzerland (in the lower Aquitanian *Molasse grise* localities; ENGESSER et al. 1993) could be related to a local meandering river system. *Diaceratherium aginense* is a large, mediportal, and rather high browser with an intermediate head holding probably depending on wet ecological niches like swamps or water beds. It is currently difficult to state whether it derives from an evolved form of *D. lemanense* or from *D. asphaltense*, since it presumably shares advanced common characters of these two species. This biozone and maybe also the MN3 biozone coincide with the only supposed Miocene spreading of the diaceratheres outside Europe, according to the occurrence of *D. askazansorensis* in southern Kazakhstan (KORDIKOVA 2001).

The end of the MN2 biozone underlines the end of the diacerathere diversification phase, whilst the increasingly warmer climate becomes wetter again. The diacerathere group is dominated by *D. aginense* and the last evolved *D. lemanense* spreading in France (Aquitaine and Paris basins) and in Germany (Rhein-hessen basin). *Diaceratherium* localities are not any more recorded in Switzerland and in south-eastern France, probably because of a palaeogeographical configuration controlled by the transgression of the perialpine Burdigalian Sea from south-western France to the Swiss Molasse Basin (OMM = *Oberer Meeresmolasse* = Upper Marine Molasse, MN2b–MN4). In the Iberian Peninsula, the FAD of *D. cf. aurelianense* is recorded in Loranca (MN2b). According to BRUNET et al. (1987), this new species probably derives from *D. aginense* and its occurrence in Spain could be linked to the geographical expansion of the latter.

The diacerathere diversity of this time interval still seems to be controlled by environments scattered in mosaic form, composed by dense to slightly open forests (*D. aginense*, *D. aurelianense*) and bushland to woodland (evolved *D. lemanense*). However, an onset to rather more closed and more humid conditions seems to be supported by the increasing gracility index of the evolved *D. lemanense* (e.g. *D. lemanense* from Budenheim, ROMAN 1924). This change of environmental pattern strengthens the hypothesis of a display of latest Aquitanian subtropical woodland type



Fig. 9. Reconstitution of the *Diaceratherium lemanense* from Eschenbach (Aquitania, eastern Switzerland). Drawing by Tayfun Yilmaz (Office de la culture, Canton Jura, Switzerland).

environments suggested by BECKER et al. (2001) in the Swiss Molasse Basin.

5.8. Stabilisation and geographical expansion (phase 3)

MN3. This biozone coincides with the beginning of the “Miocene Climatic Optimum” (BÖHME 2003). During this time interval the European diacerathere species are restricted to *D. aurelianense*. However,

they underline the greatest spreading of the group from the Iberian Peninsula to Germany and Switzerland. The occurrences in the two latter areas are restricted to the northern littoral environments of the Burdigalian Sea. *Diaceratherium aurelianense* is slightly smaller and more graviportal than *D. agnense*. It is probably a true high browser, having a head holding intermediate to up, and is adapted to forest environments close to water beds or swamps of closed woodland to rain forest types. These environ-

ments are in conformity with the closed and wet conditions suggested by COSTEUR (2005).

5.9. The typical Middle Miocene fauna

MN4. During this time interval the collision of Africa and Arabia with Eurasia closes the seaway between the Mediterranean Sea and the Indian Ocean (RÖGL 1999). A new land bridge enables a distinct mammal migration between the two continents (*Gomphotherium* land bridge of the “Proboscidean Datum Event”), resulting of an ecological bottleneck for the mammal community, because of many migration waves (e.g. African gomphotheres, Asian brachypotheres) and a stronger continental climatic control on the circum-Mediterranean lands. After BECKER (2003), northern Switzerland shows an increasing seasonality. The environments become dryer again and the humid forested areas are no longer dominating. At MN4a, the last localities of *D. aurelianense* are still recorded in Spain and in France in the north-western part of the perialpine Burdigalian Sea. The LAD of diaceratheres is recorded in the eastern part of the German Molasse Basin (*D. cf. aurelianense* from Eggingen-Mittelhart 3; MN4b) where the regression of the OMM is ended, whereas the FAD of brachypotheres is recorded in Europe with *B. cf. brachypus* from Artesilla in Spain (MN4a). After CERDEÑO (1998), the latter migrates from Asia. It probably occupies a quite different ecological niche of that of *D. aurelianense*. With its larger body size and mass, its more advanced brachypody and its lower head holding, it seems better adapted to shorter vegetation and could rather be a regular browser. After HEISSIG (1972), the brachypotheres seem well adapted to intermediary climatic conditions and not sensitive to weak changes. Even if less common, they are still present in extreme conditions (humid or dry). Thus, it could be assumed that the environments show a slight decrease of the forested area density and humidity. This fits well with the complete lost of their fifth manus digit – contrary to the diaceratheres.

At the end of this biozone, all the *Diaceratherium* representatives completely disappear, overtaken by the brachypotheres, which are at the beginning of their geographical expansion like other typical middle Miocene European taxa (e.g. *Gomphotherium*, *Lagomeryx*, *Palaeomeryx*, *Plesiaceratherium*, *Prosantorhinus*).

6. Conclusions

The study of the diacerather skull from Eschenbach presented in this paper supports its attribution to *Diaceratherium lemanense* (POMEL 1853). The description of morphological features, the comparison with other *Diaceratherium* species and the tomography analyses allow the following conclusions and comments: (1) Its back tooth pattern exhibits evolved features close to *D. lemanense* from Saint-Gérard-le-Puy and *D. aginense* from Béthusy. For these reasons we suggest the distinction between a primitive form (e.g. Gannat, Paulhiac) and an evolved form (e.g. Eschenbach, Saint-Gérard-le-Puy) of *D. lemanense*. The locality of Eschenbach seems to be older than Saint-Gérard-le-Puy (MN2a) and slightly younger than Cindré (MN1-2), thus it can be allocated to the MN2a biozone. (2) The computed tomography data and the growing state of the adult tooth eruption, compared with the ontogeny of the closest living relative (*Diceros bicornis*), suggest that the skull of Eschenbach belongs to a 5 to 7 years old specimen.

The regional level analysis of European diacerather species distribution and palaeoecology illustrates the evolutionary trends that allowed the subdivision of the Oligo–Miocene transition biogeographical context into three successive phases, plotted between two events:

(1) **The faunal renewal:** After the disappearance of the ronzother group in the beginning of the “Terminal Oligocene Crisis”, the *Diaceratherium* genus takes place in Europe (probably originating from *D. cf. lamilloquense* of Nong Ya Plong, Thailand). Currently, there is not any reasonable explanation clarifying the European latest Oligocene extinction of the *Ronzotherium* genus (and other taxa such as *Anthracotherium*). A real competition between the last *Ronzotherium* and the first *Diaceratherium* does not seem to exist. No synchronous localities are known and the arrival of diaceratheres in Europe seems really timorous (MP29, FAD with *D. lamilloquense* from La Milloque; MP30, *D. aff. lemanense* from Thézels and *D. lemanense* from Rott bei Bonn). Moreover, it is difficult to estimate the existence of a record bias because of the rather low abundance of large mammal localities during the MP29–30 interval. These primitive forms of diaceratheres are regular browsers probably occupying slightly different ecological niches, in increasingly open environments.

(2) **The diversification phase:** During the Aquitani-
an, the diaceratheres present a great diversity sup-

ported by the FAD of *D. aginense* (MN2a) and *D. aurelianense* (MN2b), the LAD of *D. lemanense* (MN2b) and *D. aginense* (MN2b), the restricted *D. asphaltense* to the MN1 biozone and the local occurrence of *D. tomerdingense* (MN1). This diversity supports a mix of regular and high browsers inhabiting different ecological niches in an environment scattered in mosaic form (bushland to forested areas). The speciation of *D. aginense* seems to take place in the Swiss Molasse Basin (upper part of the *Molasse grise de Lausanne* Formation, MN2a; e.g. Béthusy), but its derivation species (*D. lemanense* or *D. asphaltense*) has still to be clarified. Nevertheless, it is assumed that *D. aurelianense* derives from *D. aginense*. Its first record in Loranca (Spain) also corresponds to the first diaceratheres occurrence in the Iberian Peninsula. This data could suggest a late (MN2b) expansion of the diaceratheres from the Pyrenees to Spain, and also the speciation of *D. aurelianense* since there. Also, we assume the spreading outside Europe of *D. askazansorensis* in the early Miocene of southern Kazakhstan.

(3) The stabilisation & geographical expansion phase: *Diaceratherium askazansorensis* could still to be present in southern Kazakhstan, but during the Burdigalian, the European diaceratheres are exclusively represented by *D. aurelianense*. This high browser graviportal rhinoceros seems to be well adapted to forested environments close to water beds or swamps. It supports the greater geographical expansion of the group associated with the likely generalisation of Western European humid forested environments. This environmental type is no longer dominating due to the beginning of the “Miocene Climatic Optimum” which leads to aridification associated to an increasing seasonality. During the “Proboscidean Datum Event” the competition for the same ecological niche – implied by the arrival of the first European *Brachypotherium* migrated from Asia –, leads to the extinction of the diaceratheres. The first record of *Brachypotherium* cf. *brachypus* in MN4a at Artesilla (Spain) and the extension of *D. cf. aurelianense* up to MN4b at Eggingen-Mittelhart (Germany) could suggest that the first brachypotheres arrived in Europe via the Alpine Arch pathway as defined by ANTUNES (1989), but the normal European pathway cannot be excluded.

The observed evolutionary trends tend to support the appropriate time resolution of this study (biochronological units ranging in a time-scale of 10^5 – 10^6

years) for long-term change descriptions over several millions years in a phyletic lineage, although the observed morphological changes seem to be assumed at a 10^5 years time-scale. The observed environmental variations during the Western European Oligo–Miocene transition, supported by these results, are moderate and progressive, and also associated to a diaceratheres reaction mainly consisting of local extinctions, colonisation events and phyletic evolutions. On another hand, drastic palaeogeographical changes coupled with drastic environmental changes and migrations, as observed from the “Proboscidean Datum Event” and the “Miocene Climatic Optimum”, would imply a more severe faunal response coupled with faster extinction than renewal.

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